DOES EPIBIOSIS FACILITATE THE INVASION SUCCESS OF MARINE BENTHIC INVERTEBRATES?

By

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ABSTRACT

The theoretical understanding of invasion success is linked to a variety of drivers including enemy release, facilitation, and competitive ability. Within the marine environment, any bare solid substrate is quickly colonised making "free" space for settlement a limited resource. Consequently, the living surfaces of many species are subjected to the constant threat from overgrowth and/or epibiosis. Epibiosis presents a mechanism that eliminates the need to find bare space while increasing overgrowth success by settling on competitors. The ability of non-indigenous species (NIS) to see and use more types of space as "free" space may confer a competitive advantage to these species and requires greater investigation. As such the basis of this thesis is to explore epibiosis in NIS and native marine community assemblages.

Theoretically, native species have co-evolved defence mechanisms against epibiosis, whereas they are naïve against epibiosis by NIS (and vice versa). Epibiosis is common, however a systematic review revealed a lack of information comparing native and NIS interactions, especially where the outcome of epibiosis was mortality. The pattern of epibiosis was examined within naturally assembled communities to understand native:NIS epibiotic interactions. Recruitment phenology was contrasted with settlement preferences and epibiotic pressures of both native and introduced species in communities of varying ages in northern Tasmania. Native species were found to have more interactions than expected with natives than with NIS. In contrast, NIS demonstrated no significant preferences between NIS, native and bare substrates: Thus, they see all space as available, compared to native species that show a preference for type of space to settle upon.

Building on this, *ex situ* manipulative experiments were used to examine pairwise interactions controlling for propagule pressure, propagule arrival time and environmental

factors hypothesised in the literature to influence recruitment and subsequent settlement success. The experimental outcomes demonstrate that native species experience greater epibiotic settlement by both native and NIS, whereas NIS were relatively free of epibiotic load.

The multiple lines of evidence used in this dissertation have illustrated fundamental differences between marine native species and marine NIS, reinforcing the view that NIS are opportunistic settlers using a greater suite of substrates as available space than native species. Moreover, given that epibiosis generally comes at a cost to basibionts, a reduced epibiotic load on NIS compared to native competitors, infers a competitive advantage to NIS.

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GLOSSARY

Assemblage: A small functional collection of species making up any co-occurring community of plants and/or animals in a given habitat.

Basibiont: An organism that acts as substrate for an epibiont.

Bio-invasion: From "biological invasion," a broad term that describes both human mediated or natural range expansion of a species.

Cryptogenic: A species which origin is unknown. There is no clear evidence to the species being native of introduced to a specific area.

Epibiont: An organism that lives on the outer surface of another organism.

Epifaunal: Benthic fauna that lives on either hard or soft substrate, they do not live in or beneath the surface.

Incursion: The occurrence/movement of an organism into a new biogenic region to which it is not previously known to be present in.

Established: A species that has attained a self-sustaining population.

Introduction: The human mediated transfer of a species into a new recipient region (subset of invasion).

Invasion: The arrival of a species that did not evolve or historically exist in that location.

Invasive species: A species that is introduced, becomes established and causes environmental, economic, or social issues.

Non Indigenous species (NIS): An organism that is living beyond its natural bioregion. Synonyms include introduced, alien, exotic and non-indigenous.

Invasional meltdown: The establishment of one nonindigenous species facilitates the invasion success of other introduced species.

Transportation: Uptake, relocation to new geographic location and release of species to a new recipient region.

Colonisation: The process in ecology by which a species successfully integrates into a new population where it had not previously existed.

Spread: The movement beyond an existing population, or in the case of introductions, beyond the point of colonisation.

Vagility: The degree/ability to which a species can move and migrate within its environment.

CHAPTER 1.
INTRODUCTION

1.1 Background and significance

Human mediated marine biological invasions refer to both the intentional and unintentional spread of marine non-indigenous species (NIS) via anthropogenic vectors to new geographical locations, where species become established and sustain self-recruiting populations (Wotton and Hewitt, 2004). These new locations are places where the species did not evolve, resulting in a lack of co-evolutionary affinities, such as pests and diseases, that native species would typically have (Torchin et al., 2001; Torchin et al., 2003). The establishment and subsequent spread of NIS is increasingly becoming common in marine and estuarine ecosystems (Ruiz et al., 1997; Carlton, 2001b; Hewitt et al., 2004a). The diversity and richness of NIS is increasing as a result of increasing rates of human-mediated transport associated with marine recreational activities, maritime transport, aquaculture, and the live marine species trade (Ruiz et al., 2000; Hewitt et al., 2004a). NIS have modified marine ecosystems globally (Torchin et al., 2002) and have been recognised as having negative impacts on environmental, economic and social values, with the impacts to native biodiversity being rivalled only by habitat destruction (Vitousek et al., 1996; Wilcove et al., 1998; Stachowicz et al., 2002; Campbell, 2008).

Protecting values against NIS impacts requires work across the biosecurity (i.e., management of NIS) continuum of pre-border, border, and post-border management (Hewitt and Campbell, 2007). Biosecurity involves preventing introductions of NIS as well as the eradication and control of NIS that have already invaded and have established a population (Hewitt et al., 2004b). Although pre-border and border protections are desired, the increasing movement of vessels, people and goods implies that incursions (i.e., the arrival of NIS) are

inevitable. Therefore, understanding factors that facilitate the post-border settlement, establishment and spread are of immense scientific and practical interest to managers who aim to predict, mitigate and control future and present invasions (Carlton, 2001b; Hewitt et al., 2004b; Wotton and Hewitt, 2004). Research concerning these factors however, has relied on a limited suite of experiments focused on factors associated with invasion success of NIS and on the consequences that NIS impose on native communities (e.g., Lake and Leishman, 2004). The most significant body of previous work in this area focused on terrestrial vascular plants (Lake and Leishman, 2004). However terrestrial systems rarely mimic those found in the marine environment (Byers, 2000; Stachowicz et al., 2002), suggesting that a knowledge gap may exist in marine systems with regards to factors that facilitate the success of NIS.

To aid in the understanding of NIS introduction success (or failure) invasion ecologists have separated the introduction processes into component steps that focus on environmental and biological factors. Numerous variations of the invasion process are represented in the literature with varying numbers of steps. Yet the following points are commonly used to illustrate the major stages of a successful NIS introduction (Kolar and Lodge, 2001; Lockwood et al., 2005, Lodge et al., 2006):

1) Transportation: uptake, relocation to new geographic location and release;
2) Colonisation: need for suitable abiotic factors which determine survival in the new habitat;
3) Establishment: the new species is able to support a self-recruiting population; and
4) Spread: dispersal and range expansion;
5) Impacts: environmental, human health, cultural and/or economic effects.

With transport of species being high and new introductions being relatively low, it has been assumed that a small proportion of the translocated species become established and that a smaller proportion of these become invasive (cause environmental, economic or social

issues) (Richardson et al., 2000; Colautti et al., 2004). Williamson and Fitter (1996) have suggested that as a general guideline, success within the invasion process holds that ~1 in 10 translocated species will be released from the means of transport, ~1 in 10 of these will actually survive and establish a self-recruiting population in their new environment, and of these established species ~1 in 10 will spread and become invasive. This is often referred to as "The Rule of Tens" in the early invasion literature. The question that follows from this is, why do some NIS succeed and others fail during the invasion process?

1.1.1 Invasion success

One of the core objectives of invasion ecology is to elucidate factors that aid in the success or failure of NIS during the colonisation, establishment and spread stages of the invasion process. It is clear that both physical environment and biotic factors contribute to invasion success (Kolar and Lodge, 2001), hence it is imperative to quantify the relative importance that these factors have and how they facilitate invasion success. Several hypotheses exist concerning the facilitation of invasion leading to invasion success. These hypotheses include characteristics such as inoculation frequency and density (Kolar and Lodge, 2001; Lockwood et al., 2005), characteristics of the NIS (e.g., greater tolerance towards environmental stressors and disturbances) (Lodge, 1993; Lenz et al, 2011), and characteristics of the recipient communities, including native species diversity, productivity and disturbance events (e.g., storm surge creating new substrate) (Elton, 1958; Hobbs and Huenneke, 1992; Stachowicz et al., 1999; Stachowicz and Byrnes, 2006).

The size and frequency of inoculations, often grouped under the term "propagule pressure", refers to the number of individuals introduced into a new area and the number of times a new invader is released (Carlton, 1996; Colautti et al., 2006; Johnston et al., 2009). This has been identified as a strong correlate of invasion success in terrestrial and freshwater

systems for birds and fishes, respectively (Kolar and Lodge, 2001). This relationship has been hypothesised to drive ballast water mediated invasions in the North American Great Lakes (Drake and Lodge, 2004). A second hypothesis has identified invading species characteristics as the driver of invasions and has received support by numerous researchers (Ehrlich, 1989; Kolar and Lodge, 2001; Lake and Leishman, 2004; Whitney and Gabler, 2008). For example, it has been suggested that successful invaders exhibit 'weedy' characteristics such as high fecundity, high vagility (e.g., the ability to disperse or move), and small body size (Lodge, 1993). A third hypothesis has focused on the elements of the recipient community (such as the presence or absence of predators and parasites or disturbance regimes) as influencing factors of invasion success (Elton, 1958; Hobbs and Huenneke, 1992; Lodge, 1993; Cohen and Carlton, 1998; Connell and Glasby, 1999; Holloway and Connell, 2002; Torchin et al., 2003; Colautti and MacIsaac, 2004; Floerl and Inglis, 2005; Glasby et al., 2007).

One phenomenon that is repeatedly discussed within the literature is that NIS often appear more vigorous and have an increased fitness and performance in their invaded habitat, as opposed to their conspecifics in their native range or ecologically similar natives within the invaded region (Torchin et al., 2002; Grosholz and Ruiz, 2003; Colautti et al., 2004). This increased performance is often observed as the NIS reaching abnormally high population densities (Elton, 1958; Carlton et al., 1990), an increase in growth rate (Torchin et al., 2001; Matzek, 2012), or achieving greater body size than in its native range (Blossey and Notzold, 1995; Torchin et al., 2002). Reasons postulated to explain this often focus on favourable environmental conditions (Dobson, 1988), greater competitive advantage (making these species better invaders) (Callaway and Ridenour, 2004), NIS display a greater tolerance to environmental stresses (Lenz et al., 2011), or a release from natural enemies (Torchin et al., 2002).

1.1.2 Enemy release hypothesis

One hypothesis that has been readily accepted as contributing to invasion success through influencing the establishment and prevalence of NIS, is the 'Enemy Release Hypothesis' (ERH). The ERH postulates that NIS are successful because they are removed from their native environment, leaving their co-evolved natural enemies behind (e.g., predators and pathogens) and thus experience a competitive advantage over natives in their new habitat due to less regulation by enemies (Elton, 1958; Wolfe, 2002; Colautti et al., 2004). This release from harm allows the NIS to increase its local abundance, contributing to range expansion through increased emigration pressures (Keane and Crawley, 2002). The foundation of ERH is based upon three assumptions:

1) natural enemies are an important factor that contribute to regulating populations;
2) the impacts of native enemies on native species outweighs that of the impacts of native species on NIS within a new recipient region; and
3) NIS populations capitalise on the reduction of enemy impacts resulting in a competitive advantage over natives and consequently increasing abundance and distribution (Keane and Crawley, 2002; Roy, 2011).

NIS do accumulate enemies in their invaded range; however the diversity of enemies, the timing of accumulation, and the level of impacts to the invading species may not represent the same regulatory control as it does within the species native region (Torchin and Mitchell, 2004; Roy, 2011). The ERH has significant support within literature, and is one of the most cited justifications for the success and increased prevalence of invasive NIS worldwide (Maron and Vilà, 2001; Liu and Stiling, 2006). Hence it is not surprising that strong evidence illustrates the impacts enemies have on the fitness of prey/host species.

1.1.3 Competition

Competitor release has also been identified as a mechanism that contributes to invasion success (Torchin et al., 2003). This theoretical framework typically focuses on the reduced similarity between invading and native species, either through analysis of phylogenetic or functional groupings, morphological character, or some other analysis of niche differentiation (Lee, 2002).

Within the marine environment suitable hard substrate on which to settle and grow is a limited resource, and often cited to be the most important determinant of individual fouling species' growth and survival (success) (Connell, 1961; Dayton, 1971; Jackson, 1977; Xavier et al., 2008). Within these space-limited habitats, diversity is maintained through interacting roles of predation, disturbance and competition (Jackson and Buss, 1975). Physical attributes of the substrate are a major requirement for species that live attached to the surface, with the more favourable substrates being subjected to increased competition (Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Miller and Etter, 2008).

Three typical space limited benthic systems have been described where sessile epifaunal (organism that lives on submerged substrates) assemblages occur; these consist of: cryptic environments, vertical walls, and open zones of hard substrate (Jackson, 1977). Of these three substrate types, cryptic environments such as overhangs, under surfaces, cracks and crevices (generally light restricted and hidden), are commonly completely colonised, with free space being virtually non-existent (Morgans and Day, 1959; Jackson, 1977; Todd and Turner, 1988). Cryptic environments are generally dominated by colonial species, mainly sponges, bryozoans and ascidians, with high occupancy. For example, it has been estimated that 95% of cryptic environments on Jamaican coral reefs were utilised by colonial animals (Jackson, 1977).

Colonial species are significant with regards to marine invasions as they often become invasive, once they have been introduced, and have the ability to outcompete natives (Stachowicz and Byrnes, 2006; Dijkstra et al., 2007). Colonial marine animals commonly have sessile modes of life, which result in constant conflict for space with interspecific and/or intraspecific physical contact generally leading to competition, where the outcome is overgrowth (Jackson, 1977). Overgrowth is a constant threat that exists between marine organisms living attached to this limited substrate, often resulting in mortality of the weakest competitor (e.g., Jackson, 1977; Jackson, 1979). The frequency of overgrowth has been observed to be high within encrusting communities, especially where there are low levels of predation and disturbance (Callaway and Howard, 2007; Freestone et al., 2011). Therefore a species' ability to compete for primary space is strongly related to its long-term growth and survival.

Bryozoans and ascidians are the most abundant fouling colonial species (Jackson, 1977), with bryozoans of particular interest with regards to competition studies because their calcareous exoskeleton forms suitable hard substrate that can be colonised. Sessile organisms utilise many different mechanisms to deter or to interfere with success of potential competitors; these include: the growth of specialised structures that decrease or hinder overgrowth (e.g. avicularia in bryozoans); defensive behaviours (e.g., developing a raised growing margin); or mechanisms to prevent larval recruitment (e.g., incorporating heavy metals in the tunic of ascidians) (Jackson and Buss, 1975).

There are five different responses that bryozoans can exhibit when growth brings an individual into contact with an opposing bryozoan that forces competition (Gordon, 1972). These five scenarios are broadly categorised into two situations:

1) Cessation of growth at the growing edge where the opposing individuals meet, resulting in:
    a. incomplete development where the zooids remain as kenozooids; or,
    b. where a crest is left at the boundary of the two colonies.
2) Direct competition resulting in:
    a. Overgrowth of the opposing colony;
    b. overgrowth by the production of stolons by one of the opposing colonies; or, a colony may overgrow itself (Gordon, 1972).

1.1.4 Epibiosis

Within the previously mentioned space-limited ecosystems, new bare suitable substrate on which to grow is rarely created and relies on factors such as disturbance and mortality events (Levin and Paine, 1974; Hastings, 1980; Paine and Levin, 1981). As a consequence, any freed bare natural or artificial substrate quickly becomes colonised (Wahl and Lafargue, 1990). The accumulation of living organisms on wetted surfaces by adhesion, reproduction or growth is referred to as biofouling. Biofouling is generally described as a process (Railkin, 2004; Cao et al., 2011). Firstly any new substrate develops an organic layer (conditioning film) made up of organic materials such as polysaccharides and proteins which adsorb to the surface (Railkin, 2004). This conditioning film forms as a result of a simple physical reaction and results in the surface being stickier. Following this the biofilm develops as an organic layer of microfoulers adhere to the surface (mainly bacteria, protozoa, algae and fungi) (Wahl and Lafargue, 1990; Railkin, 2004). These microfoulers then promote settlement and growth of macrofoulers, such as invertebrate larvae and macroalgae spores (Patil and Anil, 2000; Dobretsov and Qian, 2002; Harder et al., 2003). Settlement however is not limited to inanimate substrates and frequently can occur on the living surfaces of marine

biota. The growth of one organism (the epibiont) on another (basibiont) is called epibiosis (Wahl, 1989).

Epibiosis is a direct consequence of limited settlement substrate, which a majority of sessile and sedentary invertebrates are subject to (Harder, 2009). Epibiosis may come at a cost or benefit to the basibiont, with factors controlling impacts being generally species specific (Wahl and Hay, 1995). Several researchers have shown positive outcomes for the basibiont, including protection (Boero and Hewitt, 1992) and increased nutrients (Wahl, 2010). However, for marine invertebrates, negative impacts are generally cited as outweighing benefits (Wahl, 1996; Laudien and Wahl, 1999; Harder et al., 2003; Harder, 2009; Wahl, 2010). The external surfaces of most sessile and sedentary species serve as a medium for exchange of numerous substances such as nutrients, waste, defensive metabolites, gas and spores or larvae (Wahl, 2010). Additionally, most types of abiotic and biotic stressors such as salinity, toxins or increased currents are usually detected at marine organism's outer surfaces. Since epibionts create a new interface between the basibiont and its external environment, they can negatively impact all of the aforementioned properties (Gutt and Schickan, 1998; Barea-Arco et al., 2001; Bers and Wahl, 2004; Farren and Donovan, 2007). For individual species, dealing with epibiosis generally involves trade-offs between tolerance and investment into defence, which utilises resources (Wahl, 2010).

Epibionts overcome the limitation of space to some extent by exploiting other species as primary space and avoiding the edge contact that typically initiates competitive responses (Keough, 1984; Wahl, 1989). Similar to bare space recruitment, individuals that live as epibionts have shown preference when choosing a settlement site (Ryland, 1974). It has been described that there is a high degree of co-evolution, adaption and specialisation between epibionts and basibionts. This can be considered especially true with regards to the epibiont, as adequate settlement ensures success and survival (Wahl, 2010). Although a majority of

epibionts do not restrict settlement exclusively to one host (Chiavelli, 1993; Wahl and Mark, 1999), some are considered to show strong selection preference based on properties of the basibionts surface (Chiavelli, 1993; Wahl, 2010). Moreover, analyses have shown that certain species of epibionts also show topographic preference when settling on a certain basibiont (Bers, 2004), often choosing substrate characteristics suited to the epibiont's requirements (Kitsos et al., 2005).

However, many benthic species exhibit opportunistic epibiosis rather than obligatory epibiosis (Wahl, 1989; Wahl, 2010). Opportunistic epibiosis represents secondary space occupancy (the settlement of a benthic species on another), when the normal circumstance would have been primary space occupancy (the settlement on inanimate substrate). Opportunistic epibiosis has been variously discussed in the literature as providing the epibiont several advantages including access to a greater amount of settlement space, thus eliminating the need to find uncolonised, bare substrate or relying on disturbance to create available space (Wahl, 1989). Similarly, settling on other species would reduce the incidence of competitive encounters and therefore enhance competitive dominance (Schneider, 2003). Conversely, the ability to avoid epibiosis would decrease the likelihood of competitive dominance through settlement. Therefore both aspects of epibiosis/basibiosis may have substantial evolutionary consequences.

Opportunistic epibiosis has been relatively unexplored as a species characteristic with the potential to contribute to the successful establishment of NIS. If the incidence of epibiosis is greater in NIS than in native species, it would likely enhance the invasion success of these species, particularly if the NIS were epibionts of native species. NIS would have a greater access to settlement space given the ability to colonise the external surfaces of other species, potentially leading to enhanced competitive dominance of these systems. Similarly, if NIS

were less likely to be basibionts (i.e., susceptible to epibiosis) than native species, they would avoid one aspect of competitive displacement.

The explicit evaluation of the incidence of epibiosis by NIS relative to natives is not apparent in the literature. Reise et al. (1999) recorded approximately 33% of NIS living as epibionts in their study of North Sea invasions. Similarly, Hewitt (1993) found the fouling NIS in his study were less likely to experience epibiosis, but more likely to be epibionts than the native species in naturally assembled communities in Oregon, USA.

1.2 Conclusion and aims

This theoretical framework infers that a NIS' ability to compete for suitable hard substrate is a determinant for success. Epibiosis is a mode of life that allows species to not only find adequate hard substrate but also eliminate competition. Herein, I propose that NIS are not only successful at exploiting this way of life, but native species also do not recognise them as suitable settlement substrate. Researchers have shown that settlement is not random and that species often recognise their settlement substrate via cues (as discussed further in Chapter 6). This implies that there is some correlation between the co-evolution of epibiont on basibiont species and settlement rates. Thus, within this work I hypothesise that due to a lack of co-evolution and substrate recognition, NIS experience a release from epibiotic pressure within their invaded range. This release from epibiosis would result in a competitive advantage.

One commonly noted mechanism to explain the successful establishment and proliferation of NIS is the reduced effect of natural enemies (Keane and Crawley, 2002; Colautti and MacIsaac, 2004). The enemy release hypothesis posits that NIS success within a new geographical region can be attributed to a decrease in regulation by natural enemies

within the introduced range compared to their native range (Colautti et al., 2004). The vast literature on enemy release generally focuses on the release from herbivores (Keane and Crawley, 2002), parasites (Torchin et al., 2003) and pathogens (Mitchell and Power, 2003). However, with the growing body of evidence into the deleterious effects that some epibionts have on their basibionts, epibionts should be considered as enemies and given that: 1) epibionts cause impacts; and 2) if epibionts exhibit settlement preference, then a release from epibiont load within a new geographical region can be viewed as a mechanism of success

Therefore, in this dissertation I will use multiple lines of evidence to illustrate the fundamental difference between native and NIS, whilst examining epibiosis as a function of NIS success. Research conducted within this dissertation examines settlement preference and settlement pressure on native and NIS benthic sessile and sedentary invertebrates, discussing the outcome in the context of competitive advantages.

As such, Chapter 1 has provided a review of the literature pertaining to factors that facilitate the success of species within sessile and sedentary benthic assemblages. Here I discussed how epibiosis may contribute to the success of NIS in a number of ways: 1) by ensuring that suitable settlement substrate is found where primary substrate is unavailable; 2) by reducing the regulating effect (reduced fitness/mortality) that is associated with having epibionts; and 3) by allowing an organism to settle on top of the species that they would have to compete with if they were to settle next to them (thus eliminating them from competitive interactions).

Chapter 2 presents a systematic review of the literature to examine associations between native or NIS epibionts with native or NIS basibionts. In doing so, I have combined data from many different works on epibiosis, and expanded these by classifying both the epibiont and the basibiont as being native, cryptogenic or a NIS. This research chapter has

been developed to investigate if there is an association between epibiont species status and the species status of their chosen basibionts.

Chapter 3 uses settlement plates to examine the recruitment of species onto bare substrate and to determine the species composition and space occupancy on substrates of varying age throughout different seasons/times (temporal analysis). The phenology of individual species is used to determine base settlement frequencies on substrates with available bare space. Research within this chapter is designed to elucidate if recruitment correlates to space occupancy and species composition.

Chapter 4 also uses settlement plates to evaluate epibiosis of native and NIS from both epibiont and basibiont perspectives. Within this chapter, recruitment is contrasted with epibiosis to explore differences in epibiotic settlement between native and NIS, as well as differences in fouling pressure. This chapter specifically aims to understand how NIS remain successful within space limited communities.

Chapter 5 explores bryozoan epibiont/basibiont interactions that were not common during the evaluation of natural communities in (Chapter 4) and used marine mesocosms (aquaria in temperature controlled settings). A manipulative experiment was undertaken ex situ to empirically evaluate differences between competing species where outcomes of competition would directly affect success.

The final chapter (Chapter 6) discusses the contributions of each chapter to the understanding of the hypothesised competitive advantage NIS have over native species. As such Chapter 6 synthesises the information presented in the thesis to present a new hypothesis for what is a facilitating factor for invasion success in marine environments.

CHAPTER 2.
A SYSTEMATIC REVIEW

2.1 Introduction

As presented in Chapter 1, there are a number of different factors that may regulate the establishment and spread of NIS. However, quantifying the relative importance of these factors has been a major challenge (Bando, 2006). Competitive interactions with resident species have impacts on NIS fitness (Corbin and D'Antonio, 2004), while simultaneously impacting on native taxa within invaded regions (Morrison, 2000; Branch and Nina Steffani, 2004). Space to settle and grow is a limiting resource for sessile invertebrate communities, and as such it is the catalyst for intense, ongoing competition (Connell, 1961; Dayton, 1971; Paine, 1974). The outcomes of competitive interactions often determine community structure (Sutherland and Karlson, 1977; Tilman, 2004).

Competitive interactions on hard substrate commonly involve overgrowth where part or all of an organism is grown over by a competing individual or colony (Jackson, 1977; Buss, 1979; Jackson, 1979). In many colonial organisms this is manifest at colony edges, with a variety of morphological responses including development of spines, large buds with increased height, and raised margins (Feifarek, 1987; Wahl et al., 1997; Harder, 2009). In some circumstances, overgrowth has little to no effect on the underlying species (Rützler, 1970; Vance, 1978). For example, growth onto the tough outer surface of many ascidians is rarely considered to have negative impacts (Claar et al., 2011). Another example is the commensal relationship between bryozoan basibionts and hydroid epibionts where the bryozoan increases food availability for the hydroid whilst the hydroid provides protection (e.g., Boero and Hewitt, 1992). However, outcomes of overgrowth interactions generally result in the mortality of the underlying species (Jackson, 1979).

Similarly, the recruitment onto the surface of another individual (epibiosis) automatically creates an overgrowth. Some epibionts have the potential to impact underlying competitors (basibionts) in very similar fashion to edge overgrowth. These impacts (both beneficial and deleterious) vary, but in general are considered deleterious as epibionts affect the external surfaces of basibionts by creating a new interface between the basibiont and its external environment (Bers and Wahl, 2004).

Research on the consequences of epibionts is vast and illustrates that epibiont/basibiont associations can have positive effects such as protection from predation and camouflage (Wahl, 1989; Wahl and Hay, 1995; Wahl et al., 1997; Gutt and Schickan, 1998; Barea-Arco et al., 2001; Schneider, 2003; Farren and Donovan, 2007). However, negative impacts such as increased predation, increased drag, competition for nutrients, and the reduction in gas exchange, are considered to be more prevalent and thus epibiosis tends to be perceived as having deleterious effects for the basibiont (McKenzie and Grigolava, 1996; Bers and Wahl, 2004) rather than positive effects. The fact that epibiosis is typically bad for the basibiont is supported by evidence that illustrates many species have developed mechanisms to deter epibiosis (Wahl 2010).

For a species to be successful within space limited, highly competitive assemblages, they must accumulate adaptions that increase their fitness (Gamfeldt et al., 2005). Natural selection theory states that favourable adaptions/traits confer greater survival and/or reproductive success, and are potentially passed down to following generations, while those with unfavourable traits have lower survival and reproductive success, leading to an eventual removal from the gene pool (Darwin, 1871). Co-evolution occurs when species have close symbiotic relationships with others, thus if one species evolves then the other species in the relationship needs to co-evolve to avoid extinction (Ehrlich and Raven, 1964). This is further expanded via the ‘evolutionary arms race’ concept that describes the evolutionary struggle

between competing species that develop adaptions and counter adaptions in an effort to out-compete each other (Dawkins and Krebs, 1979).

The evolutionary arms race is generally discussed in two different contexts, symmetrical evolution or asymmetrical evolution (Dawkins and Krebs, 1979; Brodie, 1999). Species that co-evolve symmetrically do so in a reciprocal fashion, where evolutionary forcing is typically a function of competition for a limited resource (Falster and Westoby, 2003). Alternatively, asymmetrical co-evolution involves contrasting selection pressure where one species adapts as a consequence of another species evolved traits (Dawkins and Krebs, 1979). For example, predator-prey and parasite-host interactions generally lead to asymmetrical co-evolution (Brodie, 1999).

In the case of NIS, their successful establishment, spread and increased fitness is often attributed to a release from natural enemies (Elton, 1958; Torchin et al., 2002). As discussed in Chapter 1, the enemy release hypothesis posits that, once moved to a new geographic location, invaders experience a decrease in regulation by enemies within their new region resulting from a lack of co-evolved enemies, such as predators and parasites (Elton, 1958; Wolfe, 2002; Colautti et al., 2004). Under such circumstances NIS move into areas where they are removed from the consequences of asymmetrical and symmetrical co-evolution unless their co-evolved species are introduced with them (such as via a hitchhiking community assemblage, or introduced species and their parasites). The consequences of this release are striking and have become accepted as one of the drivers of invasion success (Williamson and Fitter, 1996)

Bare space on which to settle is a limited resource, and as such is subject to intense competition. Epibiosis between two competing species may confer a competitive advantage to the epibiont as settling on top of a competitor removes it as a competitor. Additionally,

epibiosis has been shown to involve cost to the basibiont. This may be in the form of increased drag (Wahl, 1996), disrupting nutrient and waste pathways (Wahl, 2010), and /or necrosis and mortality (Harder, 2009). Hence, native epibionts on native basibionts have a long evolutionary history. This relationship can theoretically cause mortality to native basibiont species, so native basibiont species may have evolved defensive mechanisms against epibiosis. However, native basibionts that have no evolutionary history with NIS epibionts will have no specific defences against them and consequently the impacts of NIS epibionts on native basibionts may be greater.

Epibiosis allows a competitor to find suitable substrate in environments that are space limited or where bare space is non-existent by colonising a potential competitor and thus reducing the limitation of space as a resource, as well as reducing competition from overgrowth (Wahl and Lafargue, 1990; Wahl and Mark, 1999). Many benthic NIS exhibit opportunistic settlement strategies, settling on both bare space as well as living substrate, which enables the settling species to exploit other species as primary space, thus eliminating the need to find uncolonised bare substrate or having to rely on disturbances or stochastic events, such as storms, to create bare space (Jackson and Buss, 1975; Callaway and Howard, 2007). Epibiosis has been relatively unexplored as a factor contributing to successful establishment of NIS and hence is relevant to explore with respect to facilitation of invasion success.

Most invasions fail during the invasion process (Williamson and Fitter, 1996). Biotic resistance and competition for limited resources are often cited (among other reasons) as factors that regulate invasions (Elton, 1958; Levine and D'Antonio, 1999; Maron and Vilà, 2001). NIS epibionts may overcome competition for the crucial limited resource of space by having the ability to settle on both unoccupied space (the limiting resource) and living space. The latter may also act to confer a competitive advantage. Moreover, living attached to other

organisms as an epibiont releases the epibiont from the majority of contact competition, thus avoiding overgrowth and subsequent mortality.

To distinguish patterns that may contribute to the success of invasions, the research in this chapter evaluates previous taxonomic/ecological studies that have focused on epibiosis and includes an assessment of species status (native, cryptogenic (unknown origin) and NIS). By illustrating global trends exhibited by both native and NIS, this systematic review aims to identify patterns in the prevalence of basibiont/epibiont pairs based on native/NIS status without being site or species specific. It is expected that results of this chapter will show that if coevolution exists between epibiont and basibionts, that native species will have defences against the settlement of other native species, given that negative fitness impacts of epibiosis, thus reducing native epibiont on native basibionts. Similarly NIS are not expected to have a coevolved history with native or NIS and thus we expect to see similar settlement of both native and NIS on NIS living substrate. In addition, this chapter aims to determine if NIS basibiont/NIS epibiont pairs are more likely to include epibiont and basibiont species originating from the same bioregion than pairs that originate from different bioregions. Specifically, it is hypothesised that.

H1. The prevalence of native epibionts will be significantly lower on native basibionts than on NIS basibionts.

H2. There will be no difference in the prevalence of native and NIS epibionts on NIS basibionts.

H3. A greater number of the NIS epibiont/NIS basibiont pairs will originate from the same native regions than from different native regions.

2.2 Methods

To answer each of the hypotheses, a systematic review was undertaken. The procedures used for the review is outlined below:

2.2.1 Data collection and criteria for inclusion

A literature search for case studies on epibiosis using the Aquatic Sciences and Fisheries Abstracts, (was conducted arbitrarily between January 2000 – January 2011) using the combination of epibiont* OR epibiosis OR epizoite* OR epiphyt* OR basibiont* OR epizoism* OR epizoic AND marine as keywords. Only studies that fulfilled the following filter criteria were used:

1) basibiont classified to species level;
2) epibionts associated with the basibiont classified to species level; and
3) the location where species were recorded was included. This ensured that the species could be classified as native or NIS.

Studies conducted *ex situ* were not included within the study as these experiments generally involved introducing an epibiont to one or a restricted number of basibionts, thereby restricting (or forcing) settlement choice. Data analysed were restricted to benthic epibionts and basibionts, with any pelagic epibiont/basibiont associations being excluded.

All epibiont and basibiont species were categorised to native or NIS status using information from the literature on individual species known native and introduced ranges (from Hewitt and Campbell 2008 and C. Primo pers. comm.), and the location where they were found in the selected study. Locations were recorded to large scale IUCN bioregions (revised from Kelleher et al., 1995). For example, the currently recognised introduced range for *Bugula stolonifera* is: Mediterranean, North East Atlantic, South Atlantic Ocean, Arabian Seas, South Pacific Ocean, Hawaii, North East Pacific Ocean, North West Pacific Ocean,

South East Pacific Ocean, Australia and New Zealand; and its native range is: North West Atlantic and the Wider Caribbean (Cohen and Carlton, 1995; Cohen and Carlton, 1998; Ruiz et al., 2000).

2.2.2 Data analysis

Data analysed was count data based on 2 categorical variables, basibiont status (Native, Cryptogenic and NIS) and epibiont status (Native, Cryptogenic and NIS). The relationship between native/NIS epibiont/basibiont pairs was recorded and analysed using a chi-square test of independence (SPSS version 21). When an epibiont/basibiont species pair was repeatedly identified in the same bioregion, the incidence of the species pair was only recorded once. To determine the effect that the presence of cryptogenic species had on the analysis, separate analyses were conducted and presented (e.g., Figure 2.2) as follows:

1) cryptogenic species were assigned as native;
2) cryptogenic species were omitted from the analysis; and
3) cryptogenic species were assigned to NIS.

To study all interactions as well as interactions where epibiont/basibiont associates are believed to impact on the basibiont with greater negative consequences analysis was conducted 3 times.

1) on all benthic basibionts (Section 2.3.1);
2) on all sessile and sedentary basibionts (Section 2.3.2); and
3) only on bryozoan basibionts (Section 2.3.3)

The NIS epibiont and their NIS basibiont associations were analysed using chi-squared goodness of fit test to determine if the ratio of pairs that originated from the same

bioregion (e.g., both from the North West Atlantic or both from the North East Pacific) and pairs originating from different regions departed from the expected ratio of 1:1.

2.3 Results

The literature search detected 1864 documents, of which only 152 (~8.3%) papers fulfilled the filter criteria. In these papers, 1240 native epibionts and 69 NIS epibionts were reported as fouling 150 native basibionts and 25 NIS basibionts. All epibiont species recorded were either sessile or sedentary attached species (e.g., species that build tubes such as terebellid and syllid polychaetes, corophiid amphipods). Basibiont species found within the literature belonged to 11 different phyla (Table 2.1), and epibionts belonged to 12 phyla.

Table 2.1: Counts of native, NIS and cryptogenic epibionts on native, NIS and cryptogenic basibionts (basibionts grouped by phylum) in studies conducted over an 11 year period (2000-2011).

	Basibiont phylogeny group	Basibiont status	Native epibiont	NIS epibiont	Cryptogenic epibionts
Plants	Angiosperm	Native basibiont	606	20	66
		NIS basibiont	0	1	0
		Cryptogenic basibiont	0	0	0
	Chlorophyta	Native basibiont	10	0	0
		NIS basibiont	246	11	13
		Cryptogenic basibiont	2	0	1
	Heterokontophyta	Native basibiont	356	23	81
		NIS basibiont	69	4	16
		Cryptogenic basibiont	3	1	0
	Rhodophyta	Native basibiont	41	5	7
		NIS basibiont	15	4	6
		Cryptogenic basibiont	0	0	1
Animals	Arthropoda	Native basibiont	77	5	4
		NIS basibiont	42	0	2
		Cryptogenic basibiont	0	1	0
	Bryozoa	Native basibiont	101	6	6
		NIS basibiont	10	24	1
		Cryptogenic basibiont	0	0	0
	Chordata	Native basibiont	50	1	1
		NIS basibiont	1	0	0
		Cryptogenic basibiont	0	0	0
	Cnidaria	Native basibiont	13	0	0
		NIS basibiont	0	0	0
		Cryptogenic basibiont	0	1	0
	Echinodermata	Native basibiont	31	0	0
		NIS basibiont	0	0	0
		Cryptogenic basibiont	0	0	0
	Molluscs	Native basibiont	168	14	18
		NIS basibiont	21	24	22
		Cryptogenic basibiont	6	2	3
	Porifera	Native basibiont	8	0	4
		NIS basibiont	0	0	0
		Cryptogenic basibiont	1	0	0

2.3.1 Benthic basibionts

Data collected on all benthic basibionts contained 269 cases where one epibiont/basibiont pair was classified as having a cryptogenic origin (Figure 2.1). All analysis (with cryptogenic species assigned to a native status, cryptogenic species omitted and with cryptogenic species assigned to a NIS status) had significant associations where the presence of native and NIS epibionts was dependent on the native/NIS status of the basibiont ($\chi^2_{[1]} = 46.002$, $p < 0.001$; $\chi^2_{[1]} = 50.454$, $p = <0.001$; and $\chi^2_{[1]} = 27.577$, $p = <0.001$ respectively) (Figure 2.2).

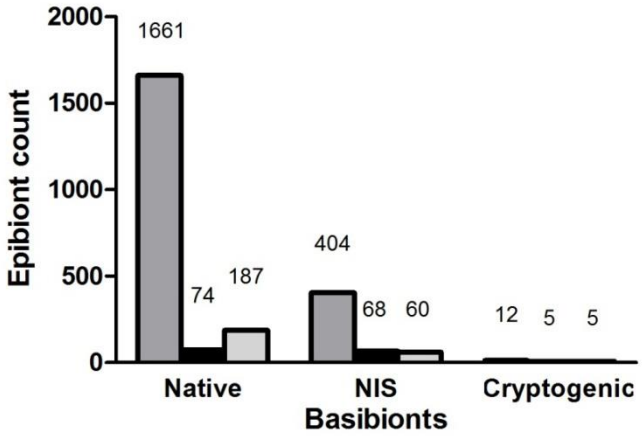

Figure 2.1: Frequency (observed number) of occurrences of native (dark grey), NIS (black) and cryptogenic (light grey) species recorded as epibionts on benthic native, NIS and cryptogenic basibionts. Note: Counts of epibionts were made from a literature search of case studies on epibiosis (January 2000 – January 2011).

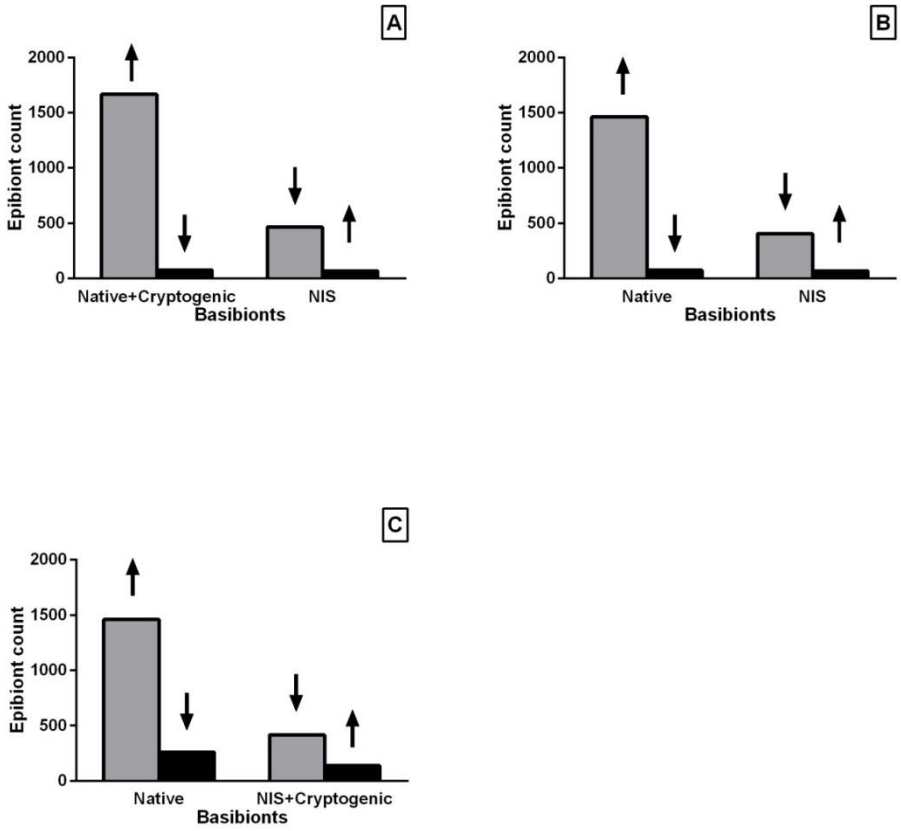

Figure 2.2: Frequency (observed number) of occurrences of native, NIS and cryptogenic epibionts/basibiont interactions on benthic basibionts, when: (A) cryptogenic species assigned to a native status; B) cryptogenic species omitted; and C) cryptogenic species assigned to a NIS status. Note: Arrows indicate categories where there were more (↑) or fewer (↓) counts of epibionts than statistically expected as determined using a chi-square test for independence. Grey denotes native species and black denotes NIS species.

2.3.2 Sessile and sedentary invertebrate basibionts

From the epibiont/basibiont pairs (Table 2.1), 668 epibiont/basibiont associations were recorded where the basibiont species was a sessile or sedentary invertebrate, of which 72 cases of epibiont/basibiont pairs contained a cryptogenic species. There was a significant association with the presence of native and NIS epibionts being dependent on the native/NIS status of the sessile basibiont for analysis with cryptogenic species assigned to native, when cryptogenic pairs were omitted and with cryptogenic species assigned NIS status ($\chi^2_{[1]} =$ 80.41, p = <0.001; $\chi^2_{[1]} =$ 102.3, p = <0.001; and $\chi^2_{[1]} =$ 107.4, p = <0.001 respectively; Figure 2.3A, B and C). More specifically, native on native and NIS on NIS relationships were observed more than expected, while natives on NIS and NIS on natives occurred less than expected .

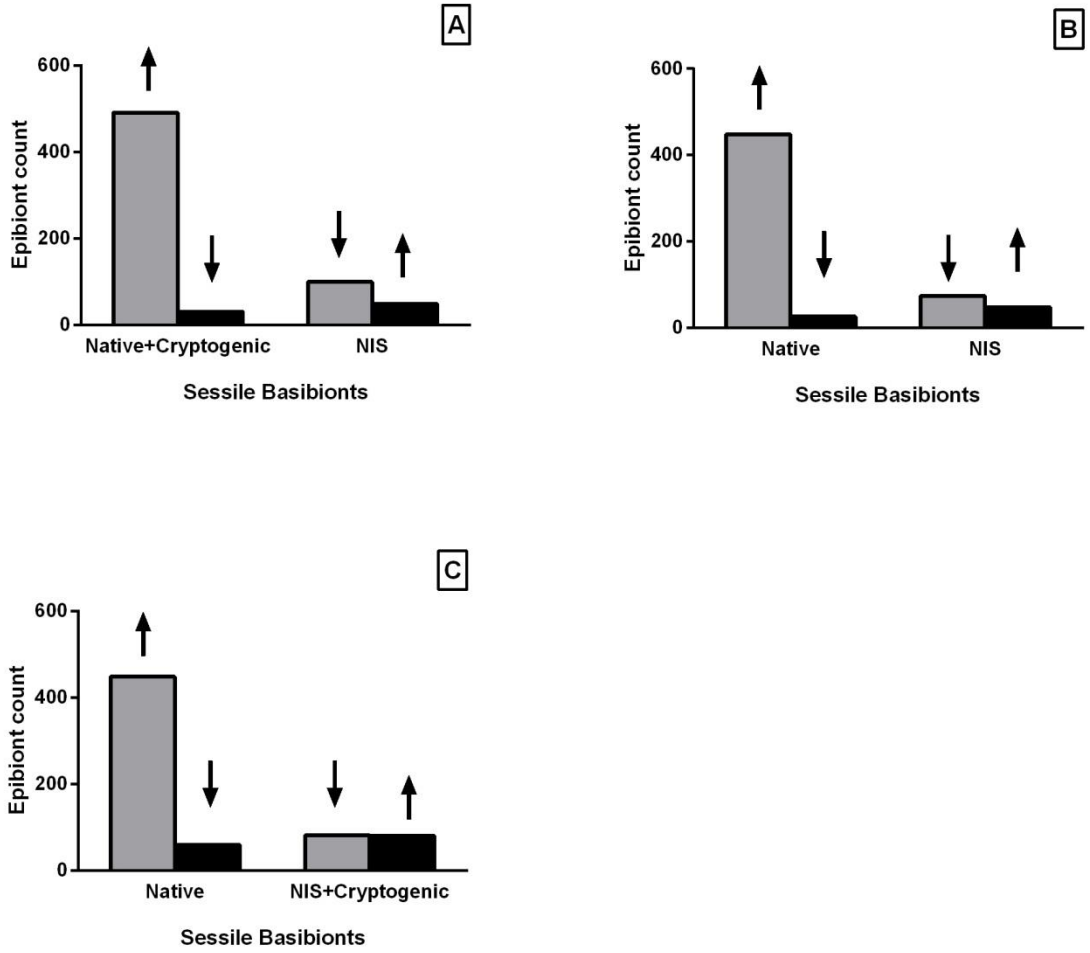

Figure 2.3: Frequency (observed number) of occurrences of native, NIS and cryptogenic epibionts/basibiont interactions on sessile and sedentary invertebrate basibionts, when: A) cryptogenic species assigned to a native status; B) cryptogenic species omitted; and C) cryptogenic species assigned to a NIS status. Note: Arrows indicate categories where there were more (↑) or fewer (↓) counts of epibionts than statistically expected as determined using a chi-square test for independence. Grey denotes native species and black denotes NIS species.

2.3.3 Bryozoan basibionts

There were 148 pairs where the basibiont was a bryozoan and of these there were 7 pairs where one of the pair's status was cryptogenic. There was a significant association with cryptogenic species assigned to native, cryptogenic pairs omitted and cryptogenic species assigned NIS status ($\chi^2_{[1]} = 66.17$, p = <0.001; $\chi^2_{[1]} = 70.32$, p = <0.001; and $\chi^2_{[1]} = 107.4$, p = <0.001 respectively; Figure 2.4A, B and C). Again the presence of native and NIS epibionts was dependent on the native/NIS status of the basibiont.

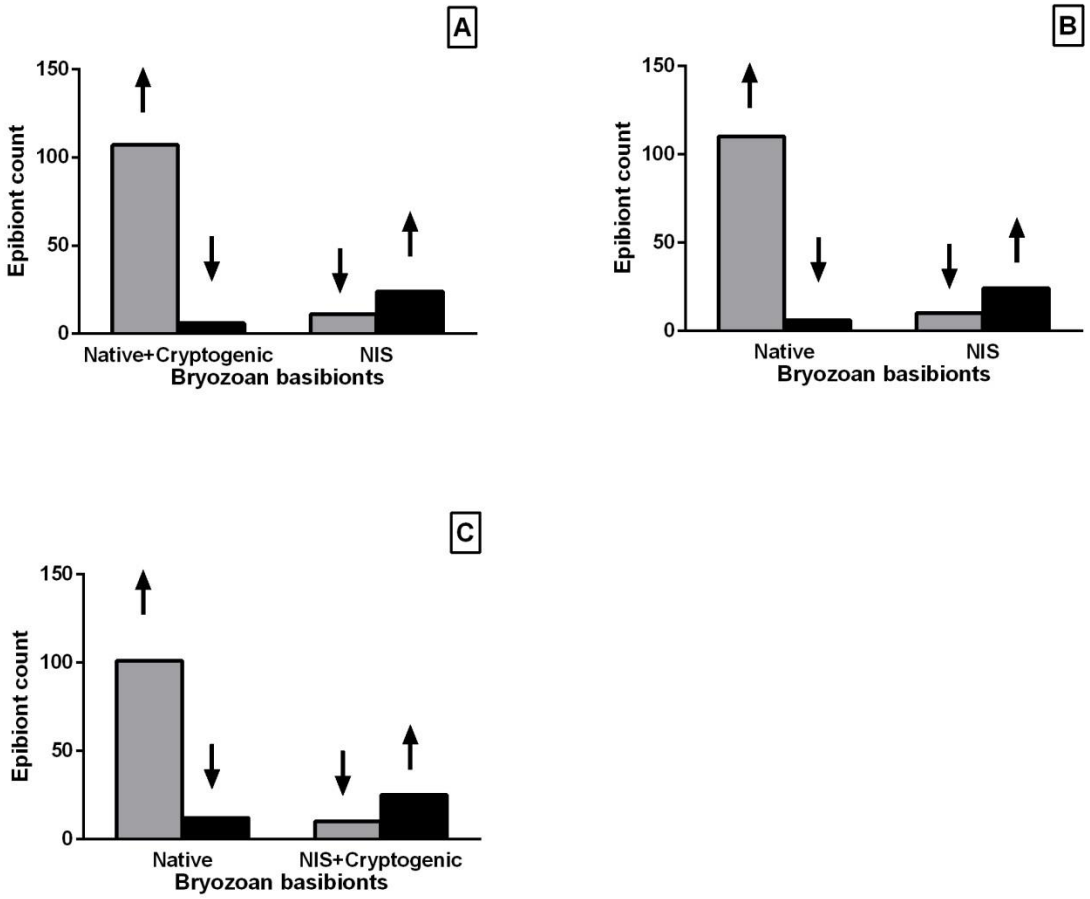

Figure 2.4: Frequency (observed number) of occurrences of native, NIS and cryptogenic epibionts/basibiont interactions on bryozoan basibionts, when: A) cryptogenic species assigned to a native status; B) cryptogenic species omitted; and C) cryptogenic species assigned to a NIS status. Note: Arrows indicate categories where there were more (↑) or fewer (↓) counts of epibionts than statistically expected as determined using a chi-square test for independence. Grey denotes native species and black denotes NIS species.

2.3.4 NIS epibiont:NIS basibiont associations

From the 68 pairs of NIS epibionts living attached to NIS basibionts, 34 pairs were identified as being native to the same bioregion. From these 34 pairs, 11 (32%) NIS epibiont/NIS basibionts combinations did not originate from the same native bioregion while 23 (~68%) did. Analysis of NIS epibiont/NIS basibiont combinations of species was statistically significant ($\chi^2_{[1]} = 4.235$; $p = 0.040$), with pairs formed by species from the same

native bioregion occurring twice as often as combinations where species were from different native bioregions.

2.4 Discussion

The use of biogenic substrates by settling species is common, and research focusing on this area is vast (e.g.,Wahl, 1989; Harder, 2009; Wahl, 2010). By combining many of these works and expanding on these by classifying both the epibiont and the basibiont as being native or NIS, this chapter aimed to identify if an association existed between basibiont/epibiont pairs based on native/NIS status (H1 and H2). Additionally, this chapter aimed to determine if NIS basibiont/NIS epibiont pairs are more likely to include epibiont and basibiont species that have originated from different native ranges (H3).

The systematic analysis in this chapter revealed an association between native epibionts and native basibionts and an association between NIS epibionts and NIS basibionts (Figure 2.2). Native species showed a strong preference to settle on native species as opposed to settling on NIS. I hypothesised that the prevalence of native epibionts will be significantly lower on native basibionts than NIS (H1) since, theoretically, it is expected that native epibiont/basibiont species pairs would have co-evolved resulting in some native basibionts having epibiotic defensive mechanisms, thus reducing epibiotic pressure (Krug, 2006). Many epibionts come at a cost to the basibiont due to increased drag, changes in buoyancy or hindering flexibility and motion (Harder, 2009). Moreover many species often rely on their external surface for important functions such as nutrient and waste exchange or photosynthesis hence, if these species external surfaces are covered, impacts may include reduced fitness and mortality (Wahl, 2010). Native epibiont species within the scope of this research settled on native basibionts at frequencies greater than expected if settlement was random (Figures 2.2, 2.3 and 2.4), thus the hypothesis was unsupported and therefore rejected. This may be due to the fact that not all epibiont/basibiont associations result in deleterious

effects to the basibiont, so epibiosis on native basibionts are still common (Wahl, 1989; Harder, 2009).

It is recognised that settlement and community dynamics are not solely a function of ocean currents, with community organisation generally being a function of larval substrate choice at a local level (Gaines and Roughgarden, 1985; Hughes, 1990). Some epibionts show a preference to settle on certain areas of specific basibiont species (Bers, 2004). For example, the barnacle *Chelonibia testudinaria* tends to settle on areas exposed to hydrodynamic currents when acting as an epibiont on *Caretta caretta*, the loggerhead turtle (Kitsos et al., 2005). Given epibionts may choose basibionts, it was hypothesised within this chapter that; the prevalence of NIS and native epibionts will be similar on NIS basibionts (H2). However, native epibiont species were recorded on NIS less than expected if settlement was random, while NIS species were recorded as epibionts on NIS basibionts more frequently than what would be expected if settlement was random (Figures 2.2. 2.3 and 2.4). Therefore, H2 is rejected.

The findings of the systematic review also support the theory of "invasional meltdown", where the previous invasion of NIS facilitates the subsequent invasion of another NIS (Simberloff and Von Holle, 1999). The positive effects of one NIS acting as substrate for another NIS species have been previously observed. Zabin and colleagues (2010) found 25 NIS living on the NIS bryozoan *Schizoporella errata,* in a location where the 25 species could not inhabit without the hard substrate provided by this bryozoan. Moreover, the invasive copper resistant bryozoan *Watersipora subtorquata* has been observed to act as a refuge for other species on the copper-based antifouling paint of vessel hulls, thus facilitating colonisation and transfer (Piola and Johnston, 2009). Biogenic substrates may also act as stepping stones for the spread of NIS with short lived larvae to other locations (Zabin et al., 2010).

Finally, I hypothesised that a greater number of the NIS epibiont/basibiont pairs will originate from the same native regions than from different native regions (H3). Unlike native species, NIS epibionts have potentially adapted (evolved) in response to a different suite of characteristics more suited to the characteristics of basibiont species from their own bioregion. Previous research has inferred that native species have a competitive advantage over NIS due to native species success with settling on natural substrates (Byers, 2002; Alpert, 2006; Tyrrell and Byers, 2007). This pattern is believed to be linked to the long evolutionary history native species have with these surfaces. This concept has generally been used to explain differences in the prevalence of native and NIS on natural versus artificial substrates, suggesting that native species have a greater association with natural substrates, while NIS are more often affiliated with artificial substrates (e.g.,Glasby et al., 2007). The research in this chapter has shown that pairs with species originating from the same bioregion occurred twice as often as pairs where the two species originated from different bioregions (section 2.3.4), thus findings within this chapter support H3.

There appears to be a strong relationship between disturbed habitats and biological invasions (Hobbs and Huenneke, 1992; Cohen and Carlton, 1998; Connell and Glasby, 1999; Byers, 2002; Holloway and Connell, 2002; Lake and Leishman, 2004; Glasby et al., 2007; Tyrrell and Byers, 2007). In fact, Chapman and Carlton (1991) explicitly identify the association of species with disturbed habitats as a criterion for recognising NIS. White and Picket (1985) include changes in resources and substrate availability in their definition of disturbance. Hence, NIS that act as a substrate for other species can be described as a disturbance because they provide new space and substrates with which natives do not have a long evolutionary history (Connell and Glasby 1999; Glasby et al 2007; Tyrrell and Byers 2007). Thus, the high observed prevalence of NIS epibionts on NIS basibionts in this study may be attributed to disturbance.

Literature focusing on invasion success is often based on a paradigm of biotic resistance. Early support for biotic resistance hypothesis was derived from observations that areas with low diversity were often highly invaded (e.g. islands). Furthermore areas that experience extinction events have also been observed to be prone to invasions (Vermeij, 1991). Initially introduced by Elton (1958), this paradigm assumes species rich ecosystems will be more resistant to invasions than ecosystems with low biodiversity (Simberloff and Von Holle, 1999).

The theoretical foundation drawn from mathematical models of community assembly suggested that communities became saturated and therefore resisted additional species entries (Post and Pimm, 1983; Levine and D'Antonio, 1999; Hewitt and Huxel, 2002). Theoretically an outcome of increase diversity would be intensified competition and greater use of common resources (Stachowicz et al., 2002; Stachowicz and Byrnes, 2006). The effects of diversity on invasion success have been experimentally examined by Stachowicz and colleagues (2002), by focusing on the success of three NIS ascidians. Experimentally results supported a theory of biotic resistance with increased survival and growth experienced by NIS in species low environments. Moreover a noteworthy observation by these researchers was that abundance of individuals had no effect. The composition of the epibiotic community may also influence the success of NIS and native epibionts through biological relationships such as competition, predation and parasitism (Torchin et al., 2003). It is acknowledged that the later may contribute to the variation in this study and it is proposed that future research focus on the temporal variation in NIS epibiont species within a community.

The study in this chapter illustrates that both native and NIS species are found on different native and NIS basibionts. However, biological and physical factors that are

hypothesised to contribute to variation within a fouling community could not be tested due to the method of data collection in this systematic review. Epibiont colonisation is often recorded as controlled by responses to chemical cues, substrate surface and even the age of the larvae (Gribben et al., 2006). The current analysis shows general trends exhibited by epibionts that are not site or species specific. However Chapter 4 expands on these findings by exploring native and NIS settlement as epibiont on native and introduced basibionts at a community level.

The data collection method used for this review does have several issues that should be noted. When undertaking a systematic review and incorporating many different works there are always inconsistencies between the published studies methods that may contribute to differences in results. Moreover a larger number of epibiosis studies were found where the host was native and it would be expected that from the pool of potential epibiotic recruits, more would be native. Simultaneously studies that focus on epibiosis on NIS often do so because they focus on NIS facilitating the success and spread on NIS (Wonham, et al., 2005; Stachowics and Byrnes, 2006). It is therefore acknowledged that the associations illustrated in this systematic review may be in part a result of the data collection methods of individual studies. Nonetheless results do however form a strong basis for the further studies within this thesis.

An additional constraint of the analyses in this chapter is that the age of the living substrate was not constant. The age of substrate inconsistency is embraced in part, as the combined case studies show trends that are not limited to a specific community age. Simultaneously, it is recognised that the age or successional state of the epibiotic community on each individual basibiont may contribute to the level of success an invading epibiont has of settling and becoming established (Klein et al., 2005).

A desired outcome of the systematic review was to record epibiotic settlement on known bryozoan invaders within their invaded regions and their native ranges in order to evaluate if invaders are released from natural enemies (epibionts) once transported to a new location (see (Torchin et al., 2003). Similar to a release from predators or parasites, a reduction in epibiosis can be considered a reduction in regulating factor that gives invading bryozoans a competitive advantage over native species. Given the strong association observed between native epibiont/basibiont pairs and the lack of preference shown by natives to choose NIS as basibionts (Figures 2.2. 2.3 and 2.4), it would be of great value to elucidate if NIS experience a release from natural enemies in the form of a reduced epibiotic load once released into a new bioregion. Differences in epibiotic pressure are examined within this dissertation (Chapters 4 and 5) however, determining the epibiotic pressure of conspecifics (of species studies for this dissertation) within their native habitat was beyond of the scope of this research.

In conclusion, there are fundamental differences between native and NIS species and their settlement patterns. Native species prefer to settle on native species, while NIS view other NIS as suitable substrate on which to settle. Hence, it would appear that native species have a competitive advantage on biogenic substrates that they have co-evolved with, and NIS epibiont success appears to be facilitated by other NIS introductions. Based on these findings, Chapters 3 will use settlement plates to study recruitment phenology to determine competitive outcomes on substrates with varying space.

CHAPTER 3.
RECRUITMENT PHENOLOGY

3.1 Introduction

One question that has generated considerable attention among ecologists is how a diverse range of species requiring the same limited resources can coexist (Ayala, 1971; Abrams, 1984). In more recent times, this question has evolved to encompass the cumulative effects/impacts of NIS (Heard and Sax, 2013). One paradigm used throughout much ecological research is that bare uncolonised space is a primary limiting resource for marine sessile invertebrates (Connell, 1961; Jackson, 1979; Ferguson et al., 2013)

Knowledge with regards to recruitment (i.e., the addition of new individuals to an assemblage; Caley et al. 1996) is essential for understanding a range of ecological phenomena including competition, population dynamics and impacts associated with NIS (Booth and Brosnan, 1995; Hughes, 1996). Studies focusing on marine invertebrates assemblages differ greatly from terrestrial systems where adults produce progeny that contribute to the community structure within the same local population (Hughes, 1990).

Species composition and density of marine sessile invertebrate communities depends on the combined interactions of many biotic and abiotic processes that influence dispersal, recruitment, post-recruitment survival, or mortality (Kunstler et al., 2007). For sessile marine invertebrates, the only opportunity for dispersal is during a planktonic larval stage (Olson, 1985). Marine ecologists long believed that the dispersal of marine sessile invertebrates was passive with ocean currents determining the spread of species throughout communities (Scheltema, 1971; Highsmith, 1980). However, several researchers have identified that many species ultimately determine final settlement locations (Woodin, 1986; Pawlik, 1992).

Traditionally, marine studies of phenology have been limited, focussing on key life history events (e.g., reproduction, settlement, recruitment) during specific time periods (time/seasons), restricted geographically, and are generally species specific (e.g., species with commercial interest) (Pickering et al., 1990). Recent studies however have refocused attention towards examining the function phenology has for competing species (Chesson and Warner, 1981; Angert et al., 2009; Edwards and Stachowicz, 2010) and its contribution to invasion success (Parker, 2001; Lee, 2002).

Population dynamics in marine invertebrate assemblages encompasses factors such as recruitment, mortality, immigration and emigration (Caley et al., 1996). Traditionally sessile marine invertebrates were generally assumed as having an open system (demographically open) where local recruitment is not a function of local reproduction (Roughgarden et al., 1985; Caley et al., 1996). Therefore, if recruitment fails, the system experiences a reduction in the density and species composition regardless of fecundity within the local population (Hughes et al., 2000). However more recent studies have argued to the importance of local recruitment, showing for many different taxa/assemblages rely heavily on local recruitment (Strathmann et al., 2002). Moreover research by Osman and Whitlatch, (1998) suggest that local recruitment can override any variation in recruitment from outside a site, thus these sites can be viewed as being closed systems.

Recruitment phenology can have a large influence on the success of both individual species and communities of benthic sessile species by influencing factors such as competition, fecundity and population growth rates associated with arrival sequence (Yang and Rudolf, 2010; Reinhardt et al., 2013). Importantly, variations in recruitment phenology may regulate biodiversity (Edwards and Stachowicz, 2012) and ultimately may be a factor contributing to NIS success (Reinhardt et al., 2013).

Recruitment of invertebrate larvae from the plankton and successful settlement is an important function that helps to determine the makeup of attached benthic assemblages (Underwood and Anderson, 1994). Recruitment depends upon a myriad of factors including propagule supply, ocean currents, stochastic events, larval predation and, very importantly, the availability of space (Underwood and Fairweather, 1989). Simultaneously, recruitment also involves species characteristics such as settlement cues (e.g., chemical, morphological and/or light cues) and larval fitness (Raimondi, 1988).

The high variability in species composition, density and distribution within marine benthic assemblages is a function of an interplay of recruitment and post-recruitment processes (Sams and Keough, 2012). Recruitment involves species characteristics and environmental factors while post-recruitment processes include predation, disturbances, facilitation and competition (Buss, 1990). Initial species composition on uncolonised space is generally a function of the available colonisers at the time the space is made available (Weiss, 1948; Sutherland, 1974; Bros, 1987), whereas in space-limited, established assemblages competition is a regulating factor (Jackson, 1977).

The loss of biodiversity, at global and regional scales, is of great concern (Hooper et al., 2005; Stachowicz et al., 2007). The introduction of new species at a regional scale will initially result in the increase in apparent biodiversity (Sax et al., 2002; Byrnes and Stachowicz, 2009), however the ultimate impact of new introductions may lead to a loss of species and the disruption of ecosystem functions. Highly diverse ecosystems are often believed to enhance the resistance of a community to be invaded (Elton, 1958; Stachowicz et al., 1999; Stachowicz et al., 2002; DeRivera et al., 2005). First coined by Elton (1958), the biotic resistance hypothesis argues that NIS success is hampered in highly diverse areas resulting from the complete use of resources (Levine and D'Antonio, 1999). This hypothesis

has grown since to also include factors such as diversity acting as a buffer against the negative impacts of an invasion (Schwartz et al., 2000).

Biotic resistance is often discussed as a function of biological interactions, with strong biological interactions often hypothesised to regulate the recruitment, establishment and fitness of NIS (Elton, 1958; Levine and D'Antonio, 1999; Freestone, et al., 2011). The biotic interactions hypothesis posits that species interactions are more common and specialised in tropical areas resulting in greater diversifications and species richness. As such biotic resistance may be stronger in tropical environments, thus explaining the reduced invasion success NIS have in the tropics (Sax, 2001). Works by Freestone and colleagues (2011) support the biotic resistance theory's, empirically showing that predation on the species richness of NIS ascidians was more pronounced in tropical locations than temperate environments.

A common mechanism of reproduction/dispersal for marine invertebrates is to release large amounts of larvae or gametes into the water column. It is estimated that a majority of a population's mortality occurs in the plankton whilst a species is in this larval stage (Thorson, 1950). Larval mortality comes from a myriad of sources which include environmental factors such as predation (Thorson, 1950; Rumrill, 1990), dissolved oxygen, salinity and pollution to name a few.

Traditionally it was assumed that the recruitment within sessile marine assemblages does not play an integral role in community structure resulting from assumptions that recruits were plentiful and that post-recruitment events are the dominant restricting factor. However, the Recruitment Limitation Hypothesis (LRH), first postulated in 1981 (*sensu* Doherty 1981), suggests that larval supply is not finite and is often a limiting factor that contributes to a populations size and density (Doherty, 1982; Caley et al., 1996).

The supply of propagules has long been linked to the invasibility of species (i.e., the potential of a species to invade). Propagule pressure refers to the size and frequency of inoculations (Carlton, 1996; Johnston et al., 2009). Propagule pressure has been shown to play an important role not only in the success of NIS, but also in the demographics of benthic assemblages (Verling et al., 2005). Variation between inoculation events greatly influences the success of invasions (Grevstad, 1999; Ruiz et al., 2000; Hewitt and Huxel, 2002).

This chapter analyses the recruitment phenology of sessile attached species, both native and NIS, living in an estuarine community in Tasmania (Australia), aiming to describe differences in the recruitment of native and NIS species, as well as differences in the temporal and seasonal variations in development after different periods of submersion. Although I refer to seasons here, please note that the experiments did not go for long enough (i.e., 3 years) to truly analyse seasonal influences and hence I have used the terminology time (or time period) to allude to a potential seasonal influence. More specifically I hypothesise that:

H4. There will be a difference in the recruitment densities of native and NIS; and

H5. Space occupied and species composition of 3 and 6-month treatments will be a function of recruitment.

3.2 Methods

3.2.1 Location

Field observations of recruitment and space occupancy were conducted at the Beauty Point marina, Tasmania, Australia. Beauty Point is a small town that lies on the Tamar River (41°17’ S, 146°57’ E), approximately 12 km South of Low Head, where the Tamar River meets the Bass Strait (Figure 3.1).

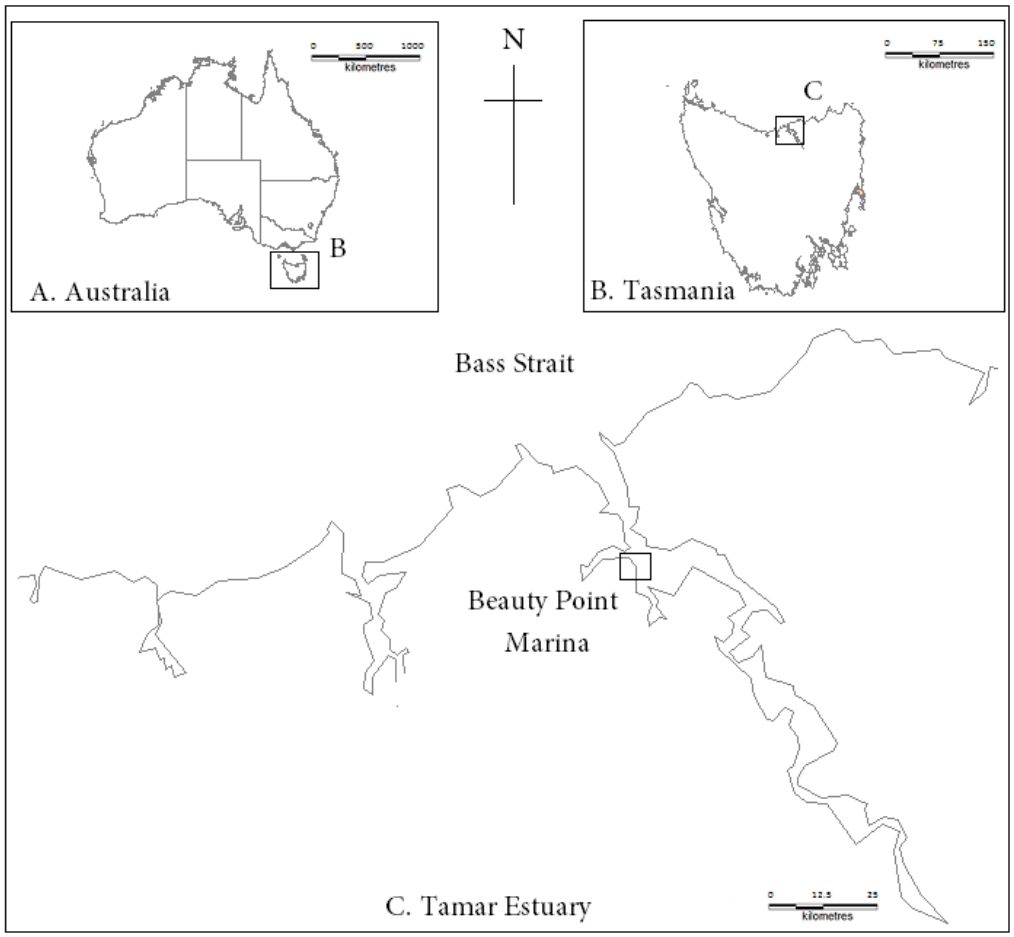

Figure 3.1. Location of study site, Beauty Point marina on the Tamar River, northern Tasmania, Australia

3.2.2 Artificial settlement collectors and deployment

Settlement collectors consisted of (14 x 14cm (196cm^2) grey Polyvinyl Chloride (PVC) plates with the exposed settlement side sanded with 120 grit sand paper to optimise conditions for attachment of organisms. Settlement plate size and material is a standard protocol in both benthic ecology and invasion ecology (Wyatt et al., 2005; Campbell et al., 2007; Sugden et al., 2008; Canning-Clode et al., 2013; Freestone et al., 2013). Settlement plates were individually attached to bricks to provide stability and weight within the water column. Individual collectors were suspended by rope from floating docks at a depth of 3m in water ~7m deep, this insured plates always remained >1m off substrate during low tide . This

placed the plates below the seasonal freshwater halocline, but retains a near surface exposure. Plates were placed a minimum of 1m apart to avoid possible bias caused by cross contamination. Plate orientation was horizontal within the water column, facing the bottom to avoid sedimentation. All settlement plates were hung in areas where they did not touch the bottom or touch other structures. Individual plates were randomly assigned to different time based treatments (i.e., months left in the water column; hereafter "treatment time").

3.2.3 Monthly recruitment

To determine recruitment of fouling organisms within the Tamar River, 10 settlement plates were deployed each month for a one month treatment time (~30 days), Deployment of settlement plates started April 2011 and final retrieval was March 2012 (Table **3.1**). All plates were marked and their location recorded so that they could be retrieved at the end of each treatment period. When retrieved, all bricks were thoroughly cleaned *in situ* (so they would not act as a source population to new plates) and 10 new recruitment assessment plates were deployed for another one month treatment time. The retrieved plates were placed in a container with seawater and transported to the laboratory for recruitment assessment. Once in the laboratory, the plates were fixed with a 10% formalin fixative buffered with seawater. After 24 hours of fixation, plates were transferred and stored in a 70% denatured ethanol solution until processing could occur, following the protocols of Hewitt and colleagues (2001). Processing consisted of removing individual plates from the ethanol solution, soaking them in freshwater for a 30min period, and identifying species and analysing abundance using a binocular dissection microscope and compound microscope when necessary.

Specimens were commonly identified to species level. In cases where this was not practical, specimens were classified to the lowest taxonomic unit (LTU) and given a morphological description so the specimens could be distinguished from others within the same group. To improve identification of species throughout different morphological stages

of the life cycle and thus aid in the identification of some species that showed different morphologies during growth, 10 plates were deployed each month for a one month period (~30 days) in similar fashion to the plates used for recruitment assessments. These plates were photographed in a consistent manner within a small tub of shallow seawater, and then returned to be suspended from the docks for grow-out (generally 2 months or until bare space became limited). In all instances photo sampling was completed in <5min and during this time care was taken to avoid damaging the fouling community. Photographed plates/photos were not used in calculating species recruitment.

All identified specimens were photographed under the stereoscope and identified with a unique code to create a voucher of each specimen type. The voucher collection enabled a quick reference of species so that morphological characteristics could be viewed and compared whilst sorting other samples. The voucher collection of individually recognised specimens (species or morphotypes) was stored in separate vessels in 70% denatured ethanol.

Once an organism was identified to species or morphotype, it was classified as having a status of either native or NIS (cryptogenic species *sensu* Carlton 1996) were treated as native because very few "true" cryptogenic species were identified, however there were many species that were unknown where a lantern binomial could not be assigned and as such the assumption was made that these species were native. Pre-existing data on NIS from the Tamar River estuary (Aquenal 2001) provided a baseline for previously recognised invasions and was used as a primary mean to identify a target list of species for consideration. Final determination of species status was derived from the data provided in Hewitt and Campbell (2008).

Recruitment of sessile fouling invertebrates was determined as specimens $cm^{-2}day^{-1}$ by dividing the number of individuals (solitary species; e.g. serpulids and barnacles) or

colonies (colonial species; e.g. bryozoans) on a plate by the size of the settlement plate ($196cm^2$) and by the number of days in the corresponding month. As a result of very high numbers in some species (hydroids and bryozoans), the recruitment of these species was estimated by randomly sampling five 2 x 2cm quadrats equating to $20cm^2$ (10.2% of total area). Random placement of quadrats was made using a 100 point grid where 5 points were randomly selected and the 2cm x 2cm quadrat was placed so that the top right corner came in contact with the selected intersection. All of the targeted species (those too dense to count) were counted inside of the quadrat. For colonial species connected by a stolon, care was taken to follow the stolon to insure colonies were counted, not individuals. Equation 1 was then used to estimate that species abundance for the whole plate:

Equation 1

$$Recruitment = \frac{(\sum_{i=1}^{5} \text{count})}{10.2\%}$$

3.2.4 Recruitment and space occupancy

In addition to one month treatment plates, settlement plates were deployed for three and six month treatments from January 2011 to the end of March 2012 (Table 3.1) to evaluate seasonal variation. These plates were deployed in similar fashion to the one month treatment plates, with 10 replicates per deployment. Cross comparisons between treatment times were made using the voucher collections to guarantee that morphotype designations (e.g., Ascidian 3) were consistent throughout the experiment.

The percentage cover of the plate where primary settlement occurred was estimated by grid point analysis. A PVC frame with 10x10 lines, creating 100 fixed (non-random) intersects, was placed over the settlement plate and the space directly under every grid intersect was

visually examined to determine if it was bare space or the point of attachment of a species. Following Wyatt et al (2005), species that were not recorded under a point intersect but were present in the plate were recorded and assigned an arbitrarily low value of 0.25% (species occupying less than 0.25% cover (<0.5cm^2) would not be expected to be consistently sampled by the grid point density used here). Percentage cover of each species and bare space detected in the point samples, as well as species from the evaluation of the entire plate were calculated using equation 2.

Equation 2

Species cover = ((No. of counts) / 100) × (100 – (0.25 × No. of species not captured))

Table 3.1: Dates of different deployment and retrieval times of settlement plates for recruitment, three month and six month treatments at Beauty Point, Tasmania. Note dates span January 2011-March 2012.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Monthly recruitment evaluation															
Three month treatment Dec-Feb															
Three month treatment Apr-Jun															
Three month treatment July-Sep															
Three month treatment Oct-Dec															
Six month treatment Jan-Jun															
Six month treatment Apr-Sep															
Six month treatment Jul-Dec															
Six month treatment Oct-Mar															

3.2.5 Statistical analysis

To determine differences in monthly recruitment and differences between individual species recruitment One-way ANOVA with Tukeys post hoc was used, or a Kruskal-Wallis with

Dunns procedures when a non-parametric test was required. Moreover, t-test or Mann-Whitney U tests were used when only two unpaired groups were present.

Analysis of community similarity using percent cover data generated from point counts were compared by multivariate analyses using the software PRIMER v.6 and PERMANOVA+. Percent cover data were square-root-transformed before analysis. Patterns between treatments were analysed by performing non-metric Multi-Dimensional Scaling (MDS) based on the ranked Bray-Curtis similarity matrix (Bray and Curtis 1957), and Permutational MANOVA. Following-a cluster analysis the similarity percentages analysis (SIMPER; Clarke 1993) was used to identify the phylum's that contributed most to the differences between different time based treatments.

3.3 Results

3.3.1 Monthly recruitment

Fifty species belonging to seven phyla (Porifera, Cnidaria, Bryozoa, Annelida, Mollusca, Arthropoda and Chordata) were recorded recruiting over a 12 month period (Figure 3.2). From these recruits, 19 species were recorded as having an exotic origin and 31 species were recorded as being native. Bryozoans and ascidians accounted for more than half of the species richness, with 20 bryozoan species and 12 ascidian species being recorded throughout the sampling period.

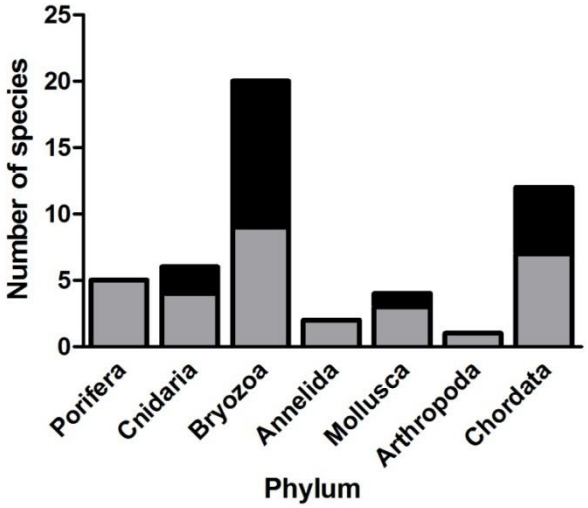

Figure 3.2: Number of species from each phylum recorded over a 12 month recruitment time sampling monthly. Note: Grey = native species, Black = NIS.

The number of combined native and NIS recruits $cm^{-2}day^{-1}$ between months differed significantly ($F_{[11, 108]} = 29.22$, $p < 0.0001$; Figure 3.3A). A Tukey's post-hoc analysis indicated that recruitment in November was significantly greater than April to September; the recruitment in December was higher than the recruitment from March to September. The recruitment in January was significantly greater than all of the other months within the tested year and February had significantly greater recruitment than July, April, and August (see Appendix C, Table 1).

Number of native recruits recorded on monthly plates differed significantly ($F_{[11, 108]} = 7.348$, $p < 0.0001$; Figure 3.3B). Further statistical analysis indicates that recruitment during the months of November to March (austral spring/summer) was significantly greater than April and July (austral autumn/winter). Moreover, November to January had significantly greater native species recruitment than August. January and November both had significantly greater native recruitment than October.

Peak monthly recruitment of only NIS occurred in January. There was a significant difference in recruitment between months ($F_{[11, 108]} = 27.02$, $p < 0.0001$; Figure 3.3C). Further analysis showed November's (late austral spring) recruitment was significantly greater than April, June, July, August and September. The number of recruits in December (austral summer) was also significantly greater than months from March to September (austral autumn to winter). January (mid-austral summer) saw the greatest recruitment being significantly greater than all other months.

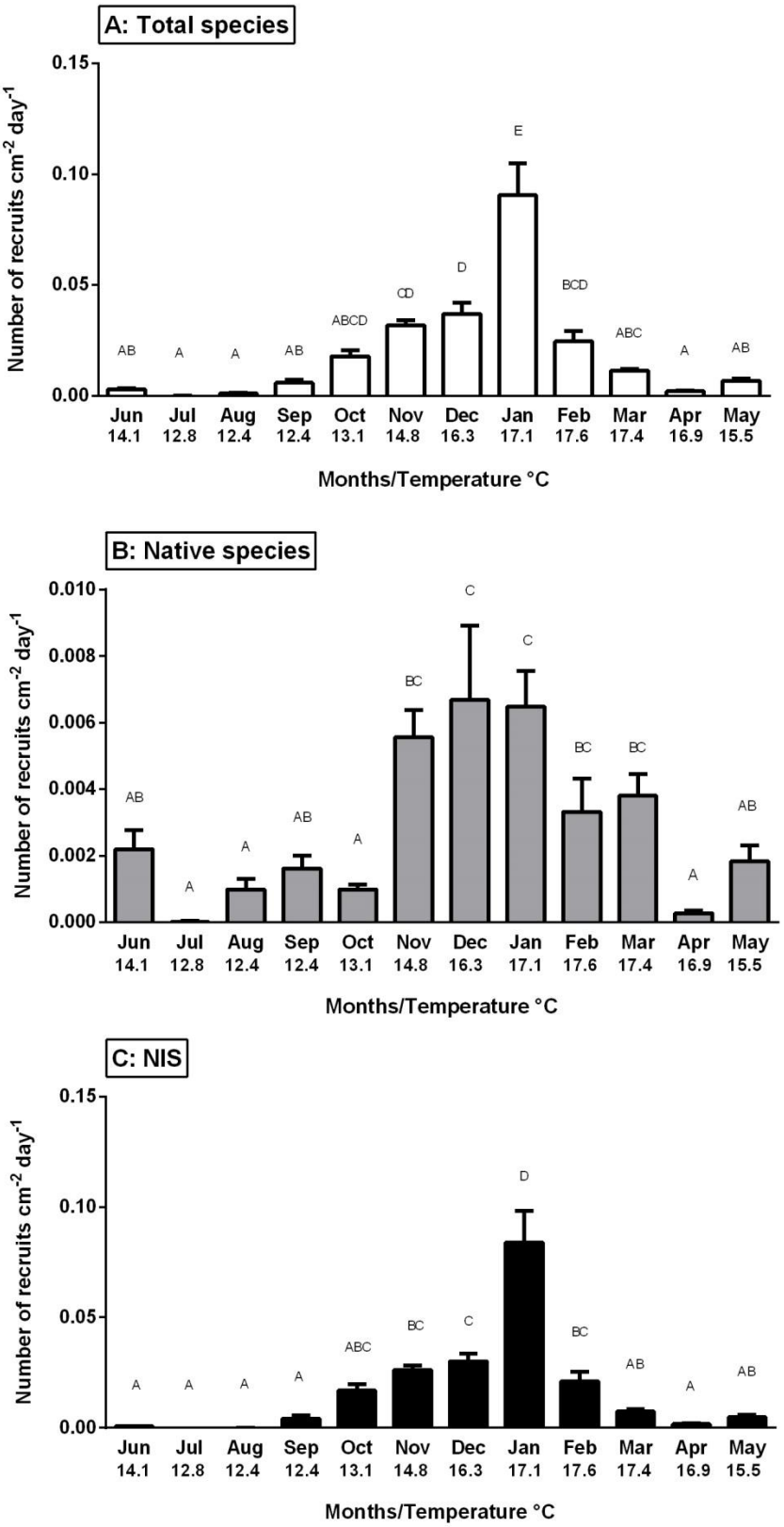

Figure 3.3: Recruitment (individuals cm^{-2} day^{-1} of sessile and sedentary species across individual months, with average temperature for each month (+SE, N=120). A= All species; B= Native species; C= NIS. Note: Letters represent significant differences between groups.

NIS recruited for an average of 4.7 months whereas natives species recruited for an average of 2.6 months. The NIS ascidians *Ciona intestinalis* (solitary) and *Botrylloides leachi* (colonial) recruited for the longest duration of time (both recruited for 10 months) and were absent only during the central winter months (July and August). Two additional NIS recruited for 8 months: the colonial encrusting bryozoan *Watersipora subtorquata* and the colonial arborescent bryozoan *Tricellaria occidentalis* (Table 3.2).

Six native species and nine NIS recruited > $7.5x10^{-4}$ individuals $cm^{-2}day^{-1}$ (herein reported as highest recruiting species) for at least 1 month. Examples of high recruiting native species included the barnacle *Elminius modestus* with high recruitment for 2 months, *Molgula ficus* which was recorded in high numbers for 4 months, and *Herdmania momus* which recruited in high numbers for 3 months. NIS generally recruited for longer periods of time; examples of NIS that recruited in high numbers are *Ciona intestinalis* (high recruitment for 6 months), *Botrylloides leachi* (high recruitment for 4 months) and *Tricellaria occidentalis* (high recruitment for 4 months).

Table 3.2: Species recorded on settlement plates across different months. Note: Different shades of grey represent number of individuals/colonies settled cm^{-2} day^{-1}. The gradient of colour increases with increased settlement base colours include lowest $=1x10^{-6}$, median $=3.75x10^{-4}$ and highest $=7.5x10^{-4}$ $cm^{-2}day^{-1}$.

Phylum	Taxa	Status	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Annelida	*Pomatoceros taeniatus*	Native												
	Spirorbid 1	Native												
Arthropoda	*Elminius modestus*	Native												
Bryozoa	*Bowerbankia sp*	Native												
	Indet Bryozoa 1	Native												
	Indet Bryozoa 2	Native												
	Caulibugula annulata	Native												
	Cellaria sinuosa	Native												
	Celleporia foliate	Native												
	Celleporia sp.	Native												
	Cryptopolyzoon wilsoni	Native												
	Membranipora sp	Native												
Chordata	*Corella eumyota*	Native												
	Didemnum moseleyi	Native												
	Herdmania momus	Native												
	Molgula ficus	Native												
	Pyura irregularis	Native												
	Pyura stolonifera	Native												
Cnidaria	*Bimeria sp*	Native												
	Eudendrium capillare	Native												
	Obelia sp 1	Native												
	Zyzzyzus spongicolus	Native												
Mollusca	*Chlamys asperrimus*	Native												
	Electroma georgiana	Native												
	Theora lubrica	Native												
	Clathrina sp	Native												
Porifera	*Darwinella sp*	Native												

Table 3.2: Continued.

Phylum	*Taxa*	Status	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Porifera	*Indet Porifera 1*	Native												
	Indet Porifera 2	Native												
	Indet Porifera 3	Native												
Bryozoa	*Amathia distans*	NIS												
	Amathia tortuosa	NIS												
	Bowerbankia gracilis	NIS												
	Bugula flabellata	NIS												
	Bugula neritina	NIS												
	Bugula stolonifera	NIS												
	Cryptosula pallasiana	NIS												
	Electra pilosa	NIS												
	Membranipora membranacea	NIS												
	Tricellaria occidentalis	NIS												
	Watersipora subtorquata	NIS												
Chordata	*Botrylloides leachi*	NIS												
	Botryllus schlosseri	NIS												
	Ciona intestinalis	NIS												
	Diplosoma listerianum	NIS												
Cnidaria	*Clytia hemisphaerica*	NIS												
	Obelia geniculata	NIS												
	Tubularia crocea	NIS												
Mollusca	*Crassostrea gigas*	NIS												

There was a significant difference in the recruitment between species for all months except for the Austral winter month of July (Table 3.3). Several native and NIS had significantly greater recruitment than other species with numerous being dominant for several months (Dunn's Appendix C, Table 2-12). Prominent examples include: the native hydroid *E. capillare* which recruited at greater numbers than all other species during the austral winter months of July and August. (Figure 3.5 and 3.6); *Tricellaria occidentalis*, a NIS arborescent bryozoan which recruited at greater numbers than a majority of the other recruiting species for the austral spring and summer months of October November and December (Figures 3.8, 3.9 and 3.10); the arborescent NIS bryozoan *Bugula stolonifera* whose recruitment was greater than numerous other species (up to nine natives and five NIS) for November and December (Figures 3.9 and 3.10); *Bowerbankia gracilis*, a NIS bryozoan that had significantly greater recruitment than other species in the austral summer months of January and February (Figure 3.11 and 3.12); and *Ciona intestinalis*, a NIS solitary ascidian that recruited strongly in the austral autumn months of March, April and May (Figures 3.13, 3.14 and 3.16).

Table 3.3. Statistical values for Kruskal-Wallis and Mann-Whitney U tests for recruitment ($cm^{-2}day^{-1}$) for individual months shown in Figures 3.4 - 3.15.

Season	Month	Statistic	DF	P value
Winter	June	**H=26.38**	9	**p < 0.0001**
	July	*U* =44.50	10	p = 0.5428
	August	**H= 8.819**	10	**p = 0.0122**
Spring	September	**H=29.65**	10	**p = 0.0010**
	October	**H=62.64**	16	**p < 0.0001**
	November	**H=133.6**	24	**p < 0.0001**
Summer	December	**H=166.3**	26	**p < 0.0001**
	January	**H=118.2**	17	**p < 0.0001**
	February	**H=64.35**	13	**p < 0.0001**
Autumn	March	**H=62.42**	12	**p < 0.0001**
	April	**H=47.32**	8	**p < 0.0001**
	May	**H=51.21**	17	**p < 0.0001**

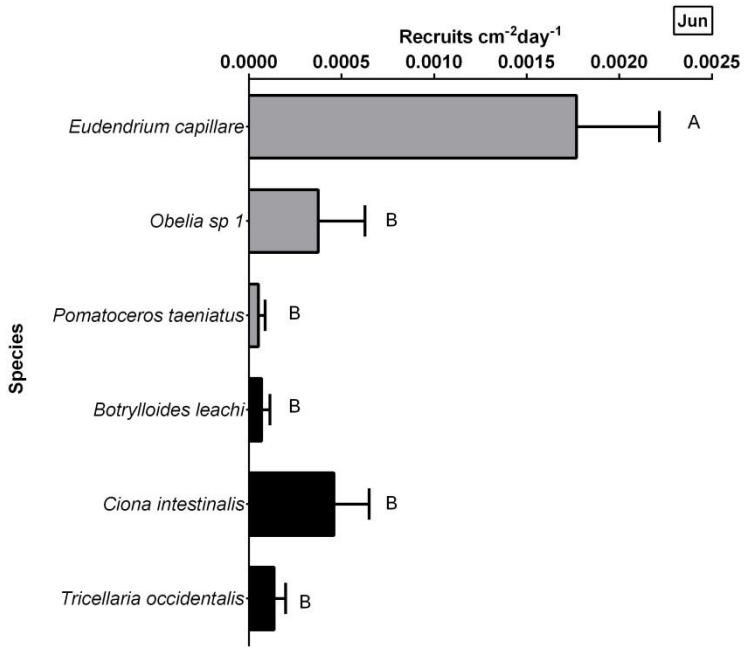

Figure 3.4: Recruitment of individual native and NIS recorded for June (+SE, N=10). Note: Grey= native species, Black = NIS, letters denote statistical significance.

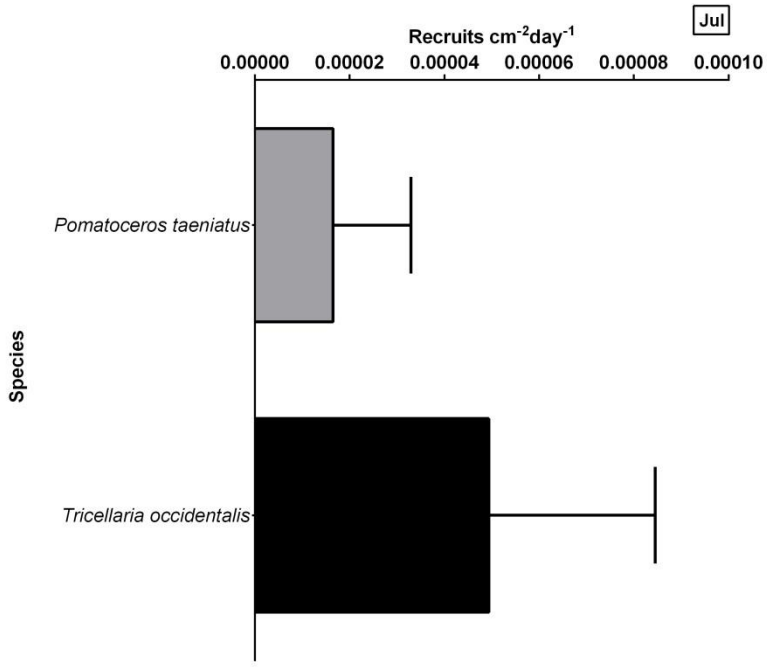

Figure 3.5: Recruitment of individual native and NIS recorded for July (+SE, N=10). Note: Grey= native species, Black = NIS, letters denote statistical significance.

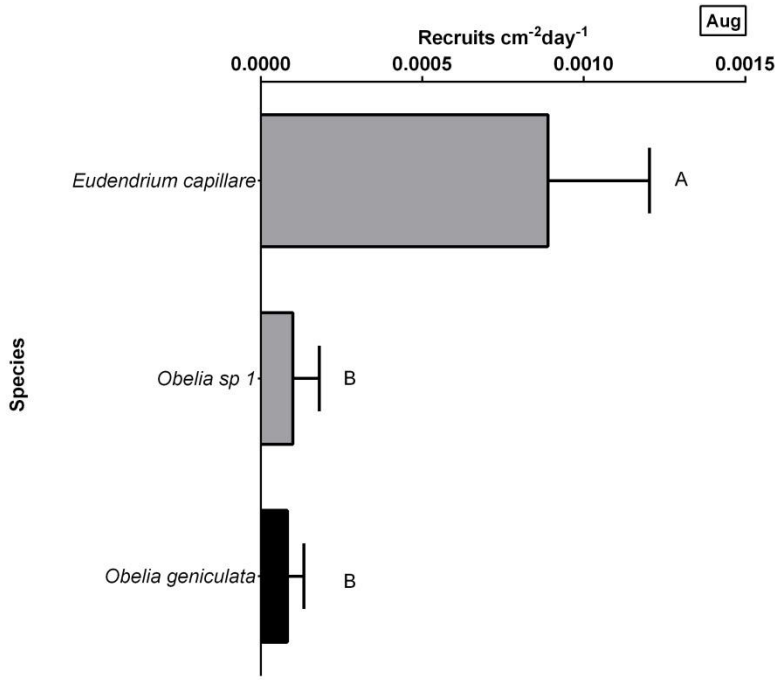

Figure 3.6: Recruitment of individual native and NIS recorded for sampling month August (+SE, N=10). Note: Grey= native species, Black = NIS.

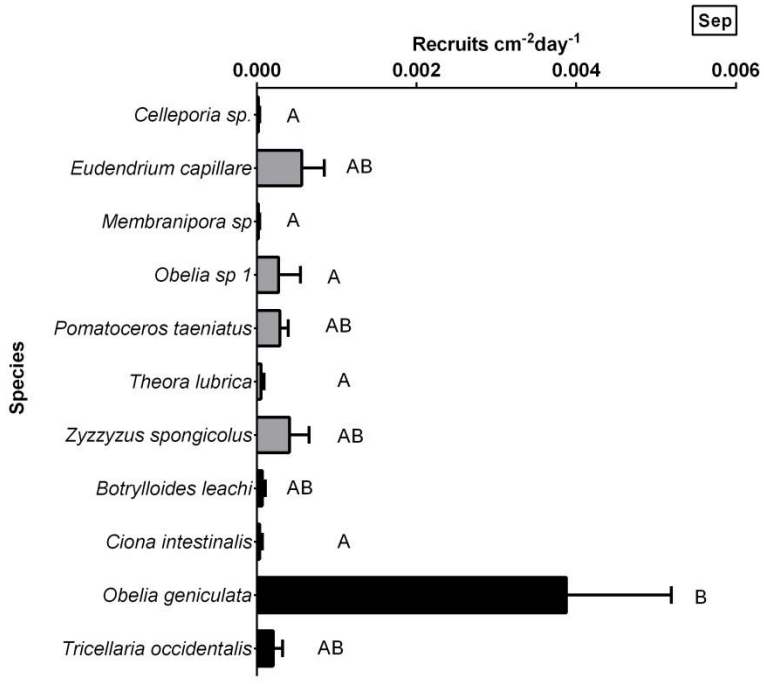

Figure 3.7: Recruitment of individual native and NIS recorded for sampling month September (+SE, N=10). Note: Grey= native species, Black = NIS.

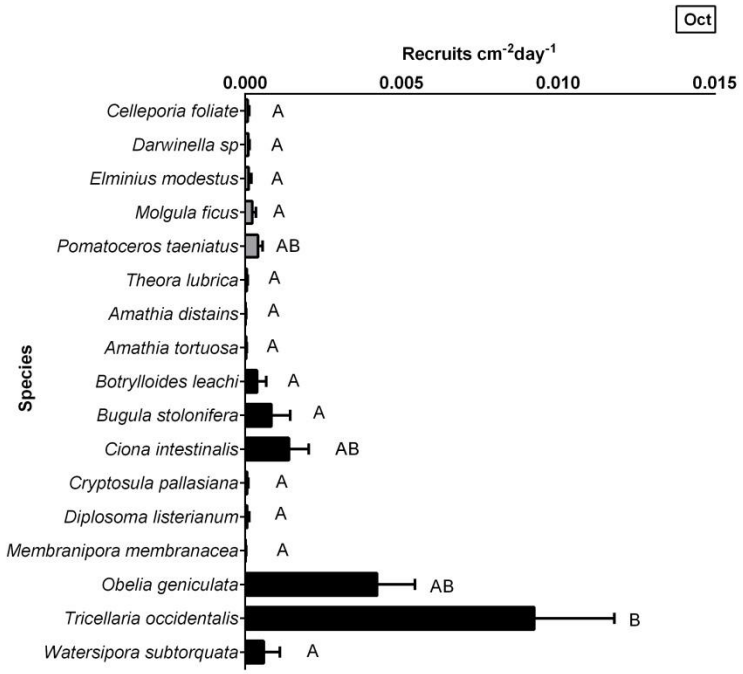

Figure 3.8: Recruitment of individual native and NIS recorded for sampled month October (+SE, N=10). Note: Grey= native species, Black = NIS.

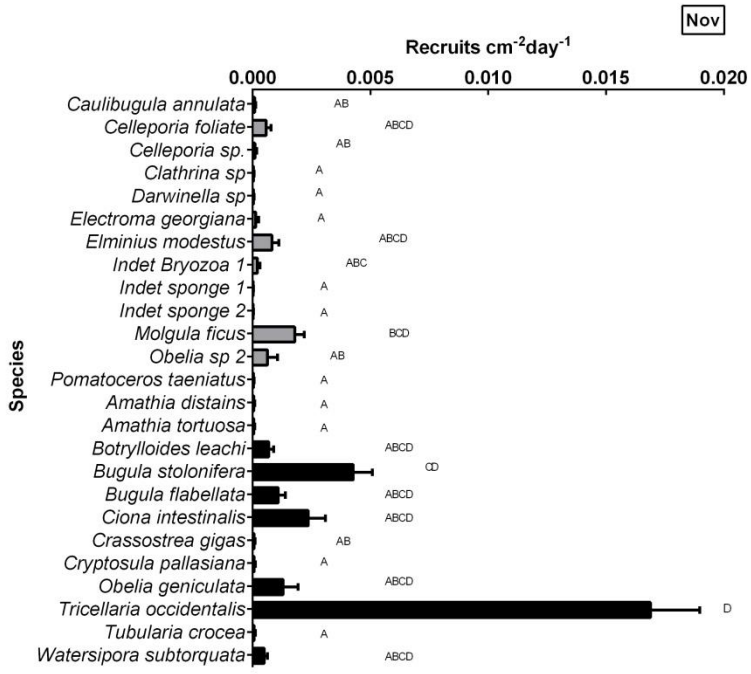

Figure 3.9: Recruitment of individual native and NIS recorded for sampled month November (+SE, N=10). Note: Grey= native species, Black = NIS.

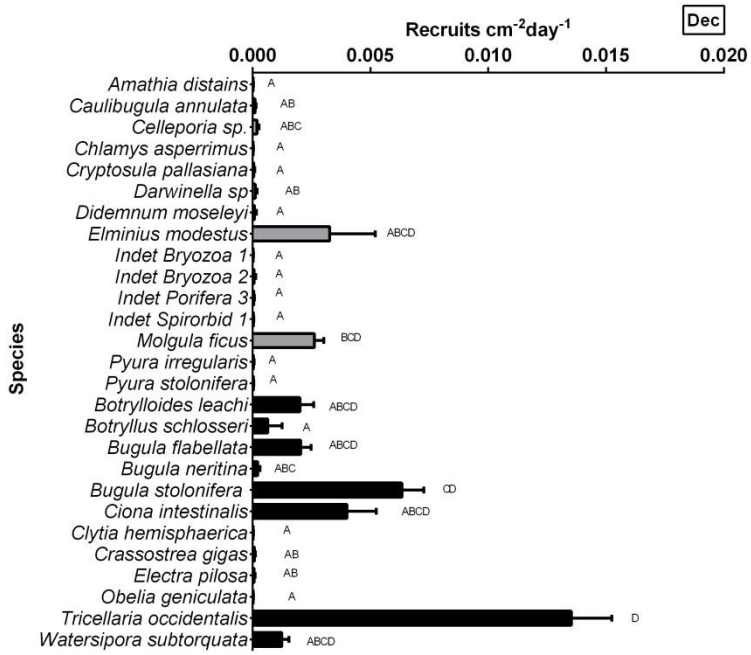

Figure 3.10: Recruitment of individual native and NIS recorded for sample month December (+SE, N=10). Note: Grey= native species, Black = NIS.

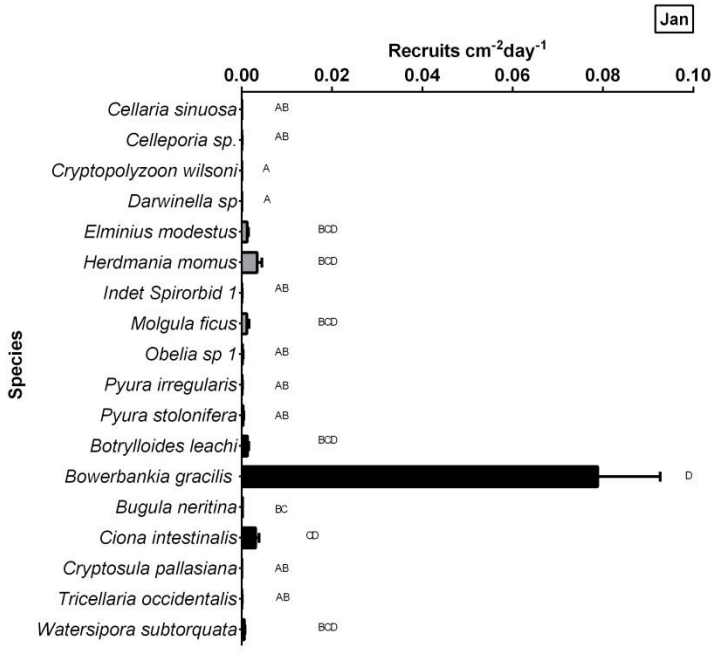

Figure 3.11: Recruitment of individual native and NIS recorded for sample month January (+SE, N=10). Note: Grey= native species, Black = NIS.

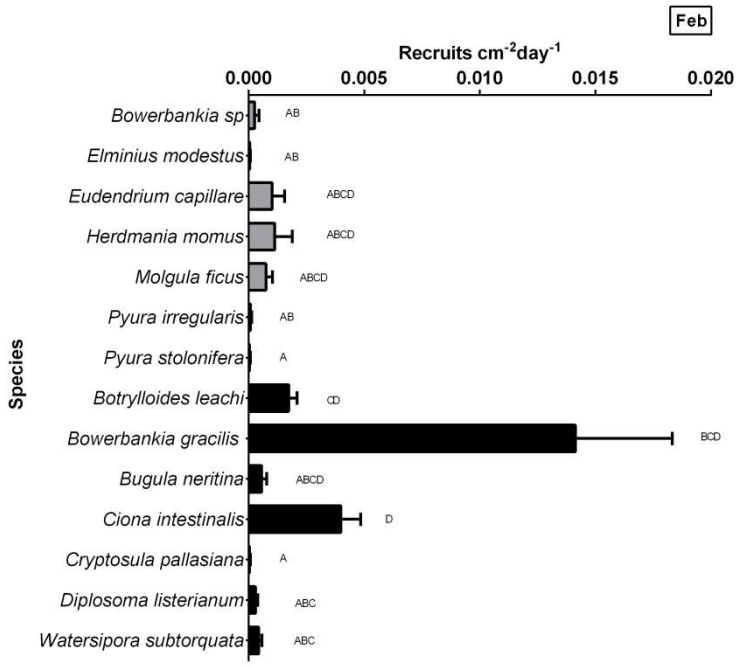

Figure 3.12: Recruitment of individual native and NIS recorded for sampled month February (+SE, N=10). Note: Grey= native species, Black = NIS.

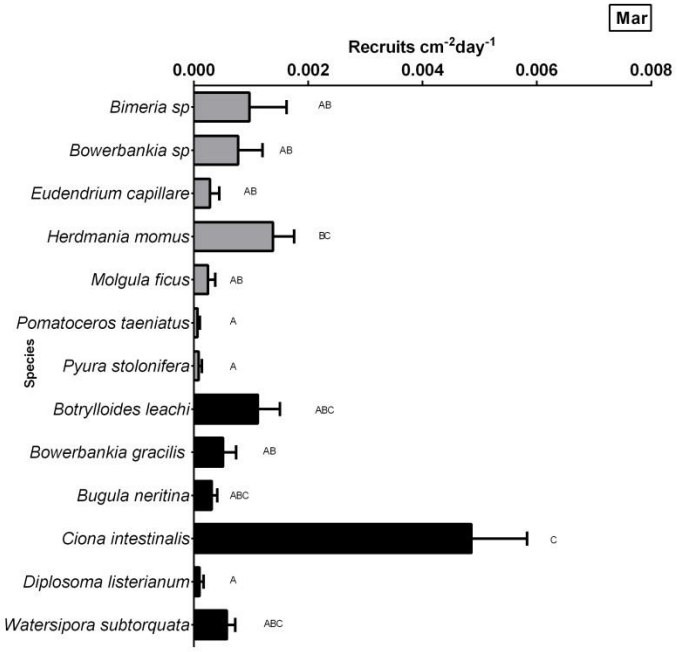

Figure 3.13: Recruitment of individual native and NIS recorded for sampled month March (+SE, N=10). Note: Grey= native species, Black = NIS.

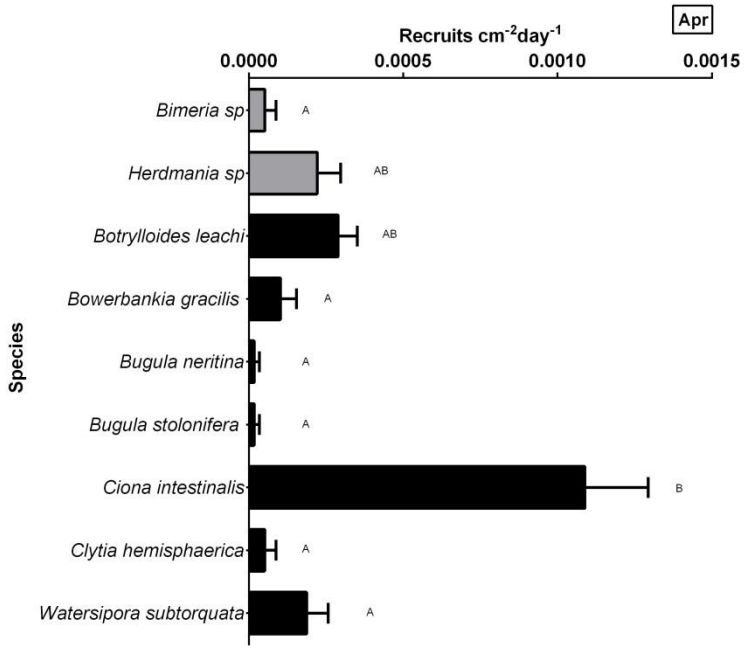

Figure 3.14: Recruitment of individual native and NIS recorded for sampled month April (+SE, N=10). Note: Grey= native species, Black = NIS.

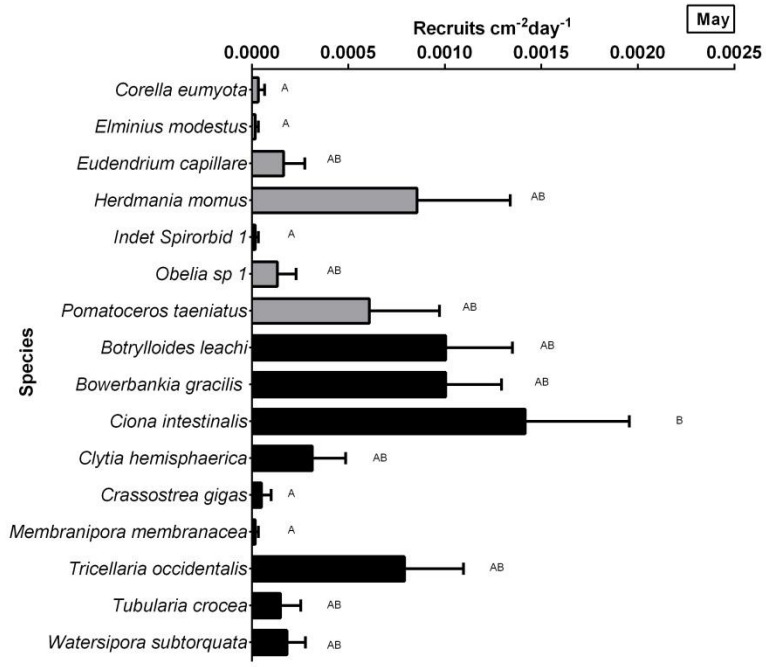

Figure 3.15: Recruitment of individual native and NIS recorded for sampled month May (+SE, N=10). Note: Grey= native species, Black = NIS.

Recruitment of native species for the month of June was significantly greater than the recruitment of NIS (Figure 3.16 and Table 3.4). Recruitment in July and September appeared to be higher for NIS species, yet there was no significant difference. Recruitment of native species in August was significantly greater (tenfold) than the recruitment of NIS. Recruitment of NIS for the remaining 8 months (October through to May) was significantly higher than the recruitment of native species over the same sample period.

Table 3.4: Statistical values for independent-samples t-tests for recruitment (cm^{-2} day^{-1}) for native and NIS species shown in Figure 3.16.

Month	Mean Native	Mean NIS	t-statistic	DF	P value
June	0.002194	0.000663	**t=2.501**	**18**	**p = 0.0223**
July	0.000016	0.000049	t=0.848	18	p = 0.4073
August	0.000987	0.000082	**t=2.853**	**18**	**p = 0.0106**
September	0.001615	0.004184	t=1.747	18	p = 0.0976
October	0.000987	0.016853	**t=5.672**	**18**	**p < 0.0001**
November	0.005561	0.026293	**t=9.236**	**18**	**p < 0.0001**
December	0.006682	0.030184	**t=5.649**	**18**	**p < 0.0001**
January	0.006484	0.084015	**t=5.403**	**18**	**p < 0.0001**
February	0.003321	0.021187	**t=4.035**	**18**	**p = 0.0008**
March	0.003802	0.007472	**t=3.293**	**18**	**p = 0.0040**
April	0.000272	0.001752	**t=5.174**	**18**	**p < 0.0001**
May	0.001827	0.004921	**t=2.689**	**18**	**p = 0.0150**

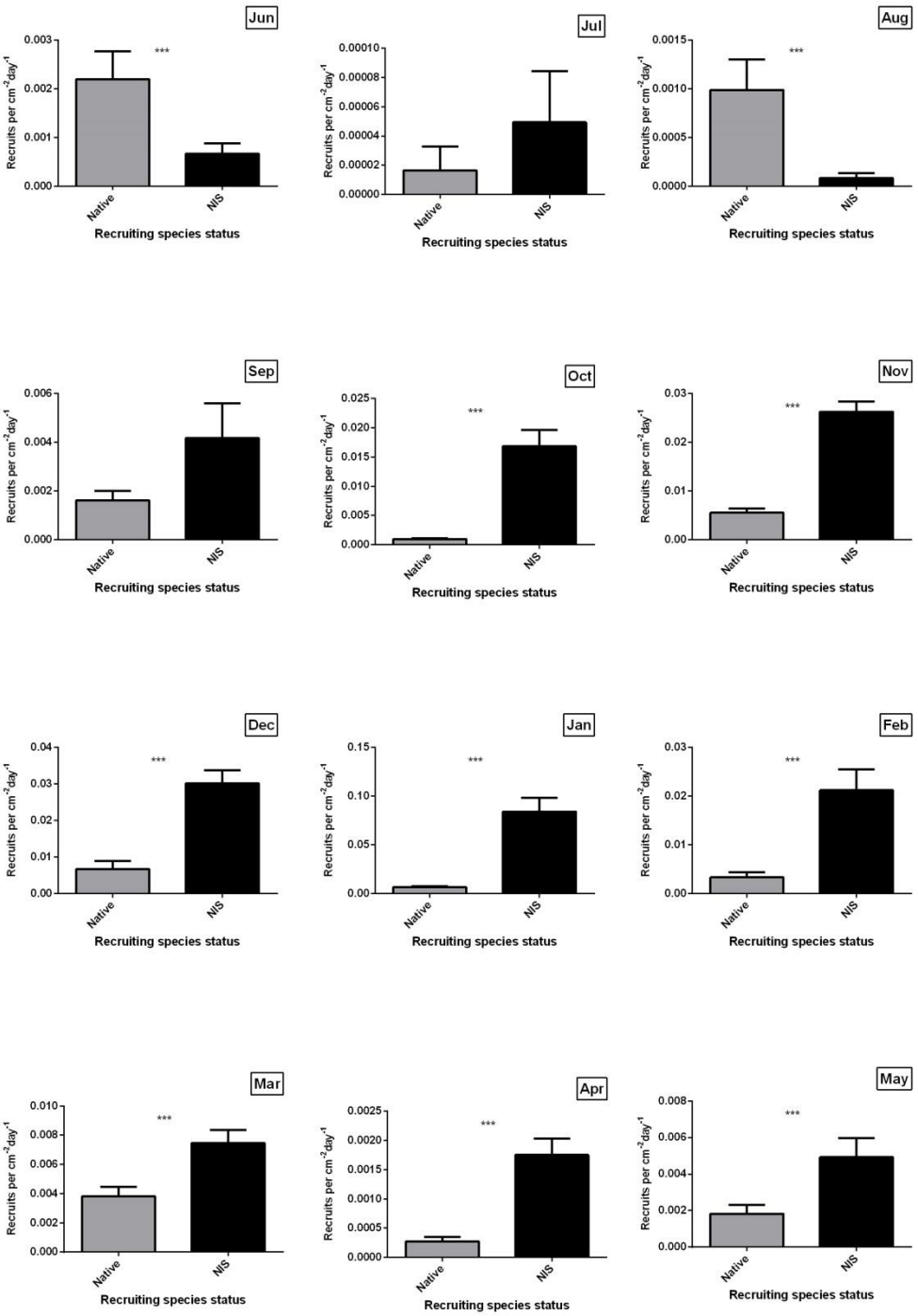

Figure 3.16: Recruitment of native and NIS species for each sampled month. Note: Y axis values differ between figures; *** represent significant differences between native and NIS recruitment (+SE, N=10).

3.3.2 Development and species composition

3.3.2.1 Species composition 3-month and 6-month treatments

Overall 34 species were recorded as recruiting and subsequently living attached to settlement plates during the three month treatments. This recruitment consisted of seventeen native species and seventeen NIS (Figure 3.17A). Fewer species (12 native and 10 NIS) recruited to the six month treatment settlement plates (Figure 3.17B).

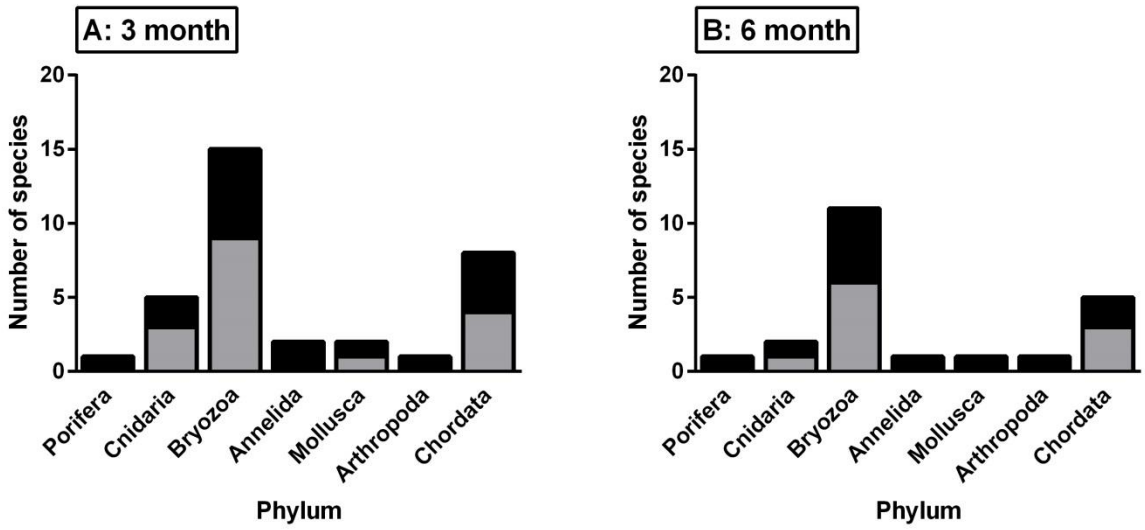

Figure 3.17: Number of species from each phylum recorded recruiting for: A) 3 months treatments and B) 6 months treatments. Note: Grey = native species, Black = NIS.

The number of NIS recorded on 3-month settlement plates was significantly greater than the number of native species for plates deployed from October to December ($t_{[18]}$ = 4.014 p= 0.0008) and April to June ($t_{[18]}$ = 2.716 p= 0.0142) (Figure 3.18A). Similarly, the

number of NIS recorded on 6-month treatment plates was significantly greater than the number of native species for October to March ($t_{[18]}$ = 2.387 p= 0. 0.0282; Figure 3.18B)

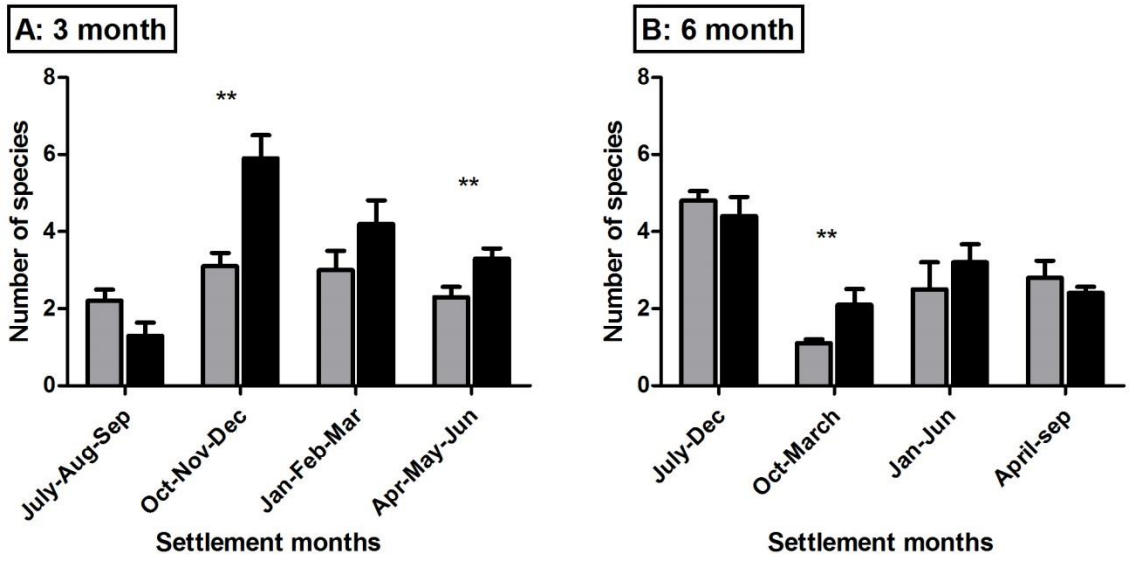

Figure 3.18. Number of native and NIS species recorded recruiting onto unoccupied space for treatments (+SE, N=10): A) 3 months; and B) 6 months. Note: Grey = native species, Black = NIS. ** above columns indicates groups that are significantly different.

Multivariate analysis of percent cover between different treatments was significantly different (ANOSIM: R = 0.668, P>0.1%). Cluster analysis and subsequent multidimensional scaling (MDS) of treatments showed that generally populations on individual plates were similar between treatments (time based deployments) (Figure 3.19). The SIMPER analysis indicated that native and NIS Chordates were dominant for most 3 and 6 month treatments, with NIS Chordates having slightly higher abundance in the 3-month treatments and native Chordates having higher abundances in the 6-month treatments. One exception was the winter 3-month treatment of July-Sep that was dominated by native Cnidarians (Table 3.5)

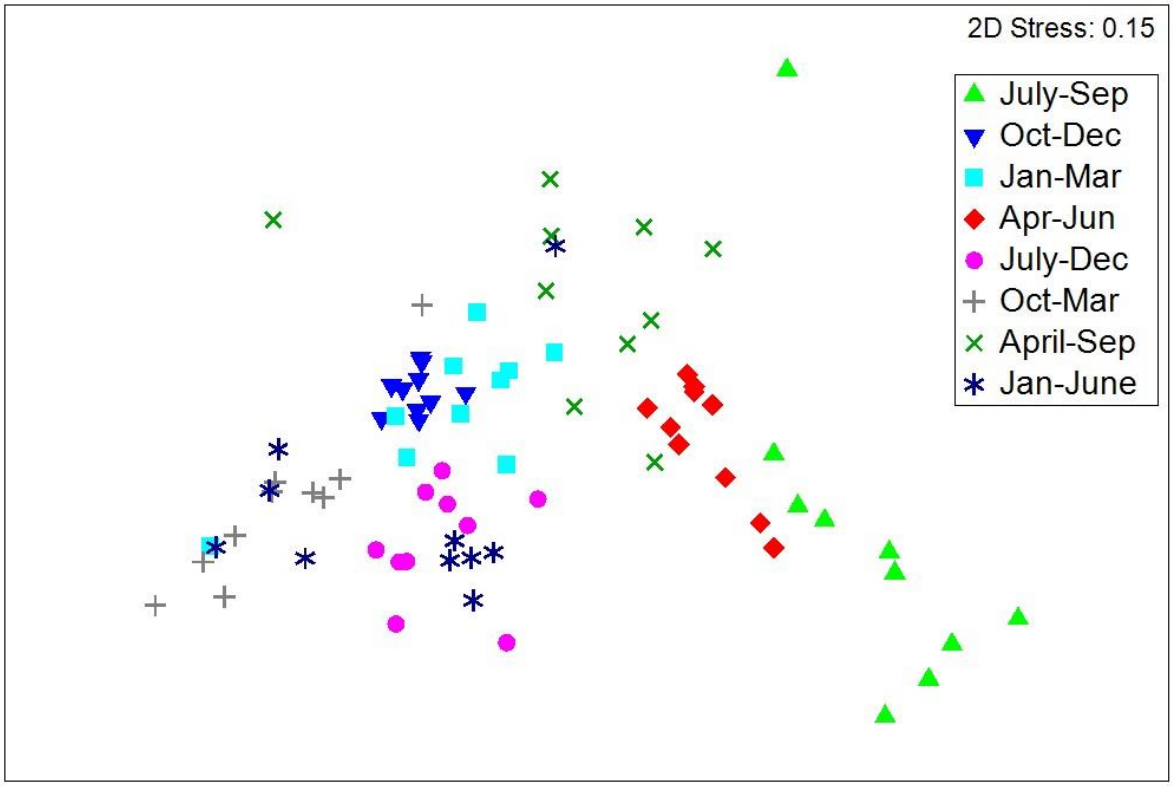

Figure 3.19: The first two dimensions of the MDS ordination plot for the percent cover of native and NIS separated into phylogenetic groups for different time based treatments.

Table 3.5: SIMPER output indicating average abundance (% cover) and % contribution to group classification (treatments) of native and NIS separated into phylogenetic groups.

	Phylum	Av.Abund	Contrib%	Cum.%
July-Sep	Native Cnidaria	35.3	70.4	70.4
	Native Annelida	08.6	12.03	82.43
	NIS Bryozoa	09.3	11.98	94.41
Oct-Dec	NIS Chordata	47.4	35.34	35.34
	Native Chordata	43.4	33.14	68.48
	NIS Bryozoa	35.9	23.73	92.21
Jan-Mar	NIS Chordata	56.2	49.94	49.94
	Native Chordata	39.3	27.36	77.3
	NIS Bryozoa	24.7	17.25	94.55
Apr-Jun	NIS Chordata	30.4	37.22	37.22
	Native Cnidaria	31.9	32.14	69.36
	NIS Bryozoa	23.1	26.09	95.45
July-Dec	Native Chordata	52.4	33.56	33.56
	NIS Bryozoan	33.3	17.77	51.33
	Native Bryozoa	29.5	17.7	69.03
	NIS Chordata	25.7	13.57	82.61
	Native Annelida	18.6	10.56	93.17
Oct-Mar	Native Chordata	83.4	81.28	81.28
	NIS Chordata	27.3	15.71	96.99
April-Sep	NIS Chordata	31.4	49.98	49.98
	NIS Bryozoan	25.9	39.43	89.41
	Native Chordata	06.	4.19	93.6
Jan-June	Native Chordata	73.9	55.43	55.43
	NIS Chordata	39.4	30.08	85.51
	Native Mollusca	14.3	5.18	90.69

3.3.2.2 Recruitment/cover on 3-month treatments

Space occupied by both native and NIS grouped together for 3-month treatments differed significantly between different deployment periods ($F_{[3, 36]} = 46.59$, $p < 0.0001$; Figure 3.19A). A Tukey's post-hoc analysis indicated that the treatment months Oct-Dec and

Jan-Mar both had significantly higher recruitment/cover than Apr-Jun and Jul-Sep (Tukey's Appendix C, Table 13). Analysis of native recruits only, showed no significant differences ($F_{[3, 36]} = 1.289$, $p = 0.2929$; Figure 3.19B), while analysis of NIS only recruitment did significantly differ between deployment periods ($F_{[3, 36]} = 30.90$, $p < 0.0001$; Figure 3.19C). Further analysis showed similar trends to when both native and NIS species are grouped (see previous Figure 3.19A) with recruitment in Oct-Dec and Jan-Mar both having significantly higher recruitment/cover of NIS than Apr-Jun and Jul-Sep sampling periods.

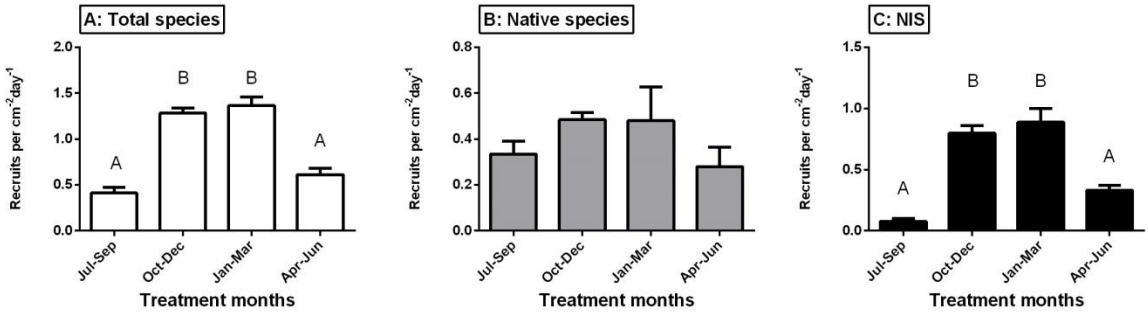

Figure 3.20: Recruitment of sessile and sedentary species for the 3-month settlement treatment for the various species grouping (+SE, N=10), when: A) All species; B) Native species; and C) NIS species. Note: Letters represent significant differences between groups; white denotes all species, grey denotes native species and black denotes NIS.

3.3.2.3 Recruitment/cover of individual species on 3-month treatments

At a species level recruitment of individuals onto settlement plates differed significantly for all of the 3-month treatment periods ($H_{[7]} = 32.82$, $p < 0.0001$; $H_{[21]} = 140.8$, $p < 0.0001$; $H_{[18]} = 94.61$, $p < 0.0001$; and $H_{[9]} = 63.48$, $p < 0.0001$ respectively; Figure 3.20A and B; and 3.21A and B).

For the 3-month treatment July-Sep, the native species *Eudendrium capillare* had significantly higher recruitment than three of the native and two of the NIS (Figure 3.20A). The treatment of Oct-Dec had three NIS with significantly greater recruitment than six of the other NIS and seven of the native recruits (Duns Appendix C, Table 14-17). Moreover the native solitary ascidian *Molgula ficus* recruited at a significantly greater rate than eight of the native species and seven of the NIS in the same period (Figure 3.20B).

For the 3-month treatment of Jan-Mar, the native ascidian *Molgula ficus* had significantly greater recruitment than eight native species and five NIS. Moreover the introduced ascidians *Ciona intestinalis* and *Botrylloides leachi* had significantly higher recruitment than eight natives and six NIS, and three native species and one NIS (Figure 3.21A).

Two of the native species, *Eudendrium capillare* and *Obelia* sp., had significantly greater recruitment than one of the native species and three of the NIS for the Apr-Jun treatment. Furthermore, the NIS colonial ascidian *Ciona intestinalis*, had significantly greater recruitment than two of the three native species and four of the NIS (Figure 3.21B).

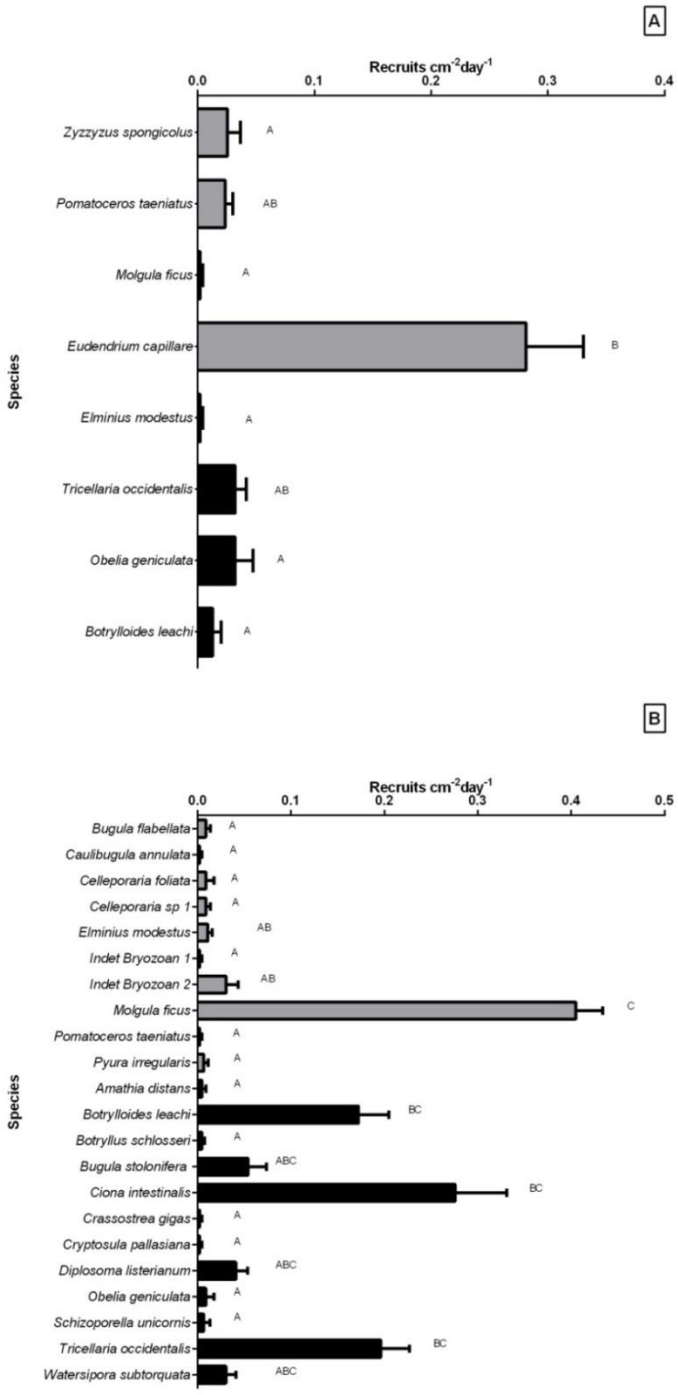

Figure 3.21: Recruitment of individual native species and NIS during the 3-month treatments for four different seasons (+SE, N=10): A) July-September; and B) October-December. Note: Grey = native species, Black = NIS

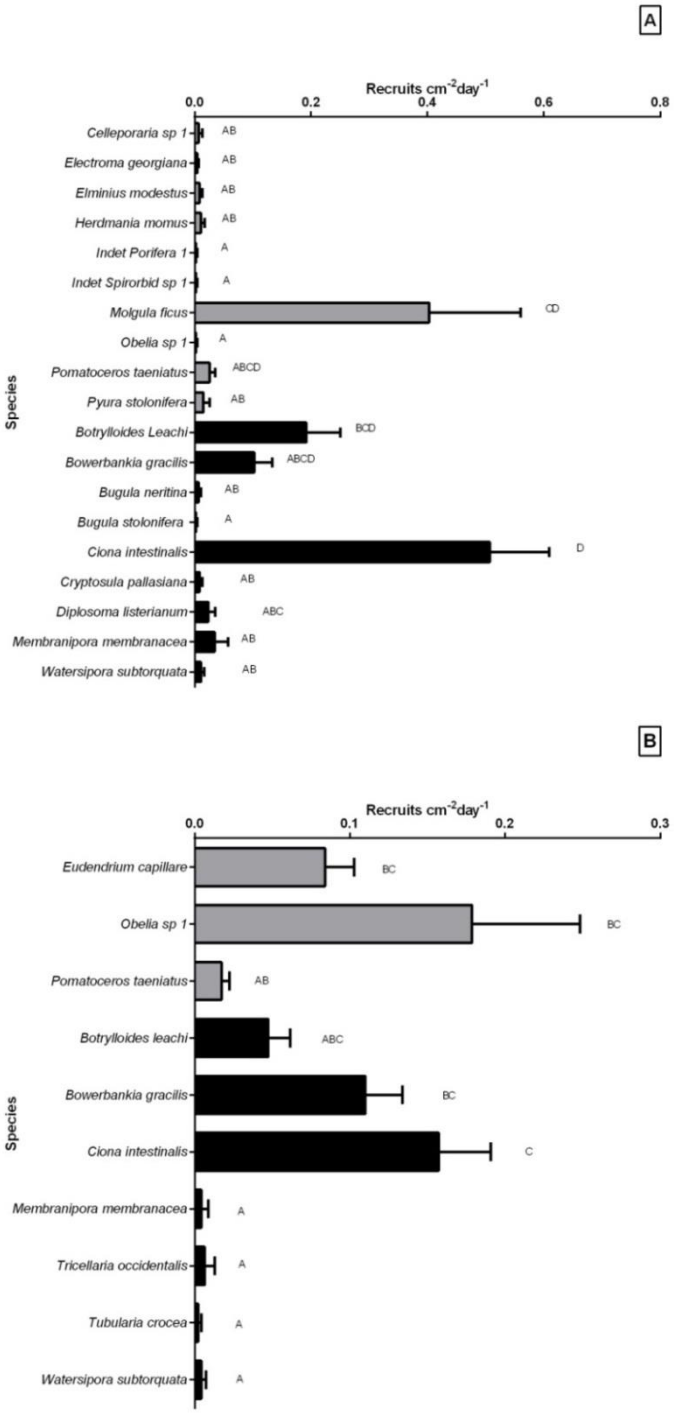

Figure 3.22: Recruitment of individual native species and NIS during the 3-month treatments for four different seasons (+SE, N=10): A) January-March; and B) April-June. Note: Grey = native species, Black = NIS

3.3.2.4 Recruitment/cover of native versus NIS on 3-month treatments

Recruitment of the all native species was significantly greater than the recruitment of all NIS for the 3-month treatment period of Jul-Sep ($t_{[18]=}$ 4.213, p = 0.0005). Recruitment of NIS was significantly higher for two of the treatments, Oct-Dec and Jan-Mar ($t_{[18]}$ = 4.529, p = 0.0003; and $t_{[18]}$ = 2.178, p = 0.0429 respectively; Figure 3.22). There was no significant difference between native and NIS recruitment/cover for the sampling period of Apr-Jun ($t_{[18]=}$ 0.5499, p = 0.5892).

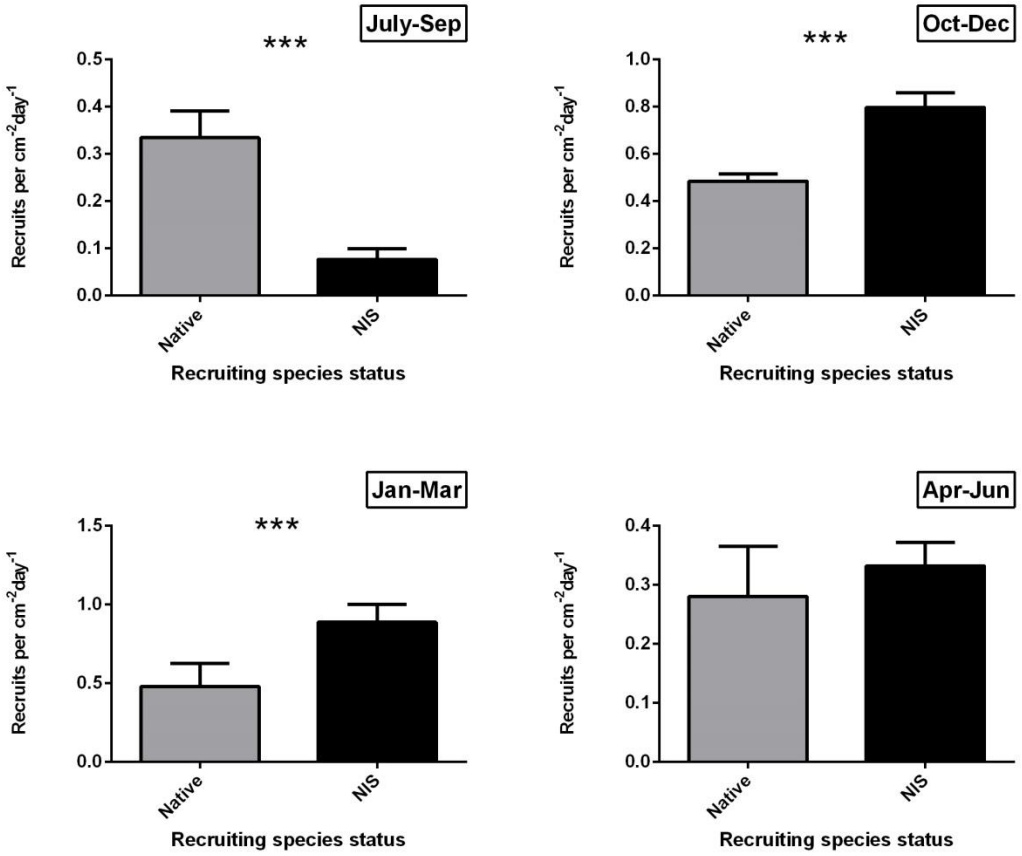

Figure 3.23: Recruitment of combined native and NIS species across three month treatments (+SE, N=10). Note: *** above columns represent significant differences between these variables.

3.3.2.5 Recruitment/cover on 6-month treatments

Recruitment and space occupied by all species combined for 6-month treatments differed significantly between deployment times ($F_{[3, 36]} = 20.94$, $p < 0.0001$; Figure 3.23A). A Tukey's post-hoc analysis revealed that the treatment months of Apr-Sep had significantly lower recruitment than the other three deployment periods. Oct-Mar had significantly higher recruitment than Jan-Jun (Tukey's Appendix C, Table 18).

Native species only recruitment between different deployment periods was significantly different ($F_{[3, 36]} = 20.68$, $p < 0.0001$; Figure 3.23B), with Oct-Mar having significantly greater recruitment than the other three periods. Additionally, the deployment periods of Jul-Dec and Jan-Jun had significantly greater native recruitment than Apr-Sep. In contrast, the analysis of NIS only recruitment did not differ significantly between different deployments ($F_{[3, 36]} = 1.067$, $p = 0.3753$; Figure 3.23C).

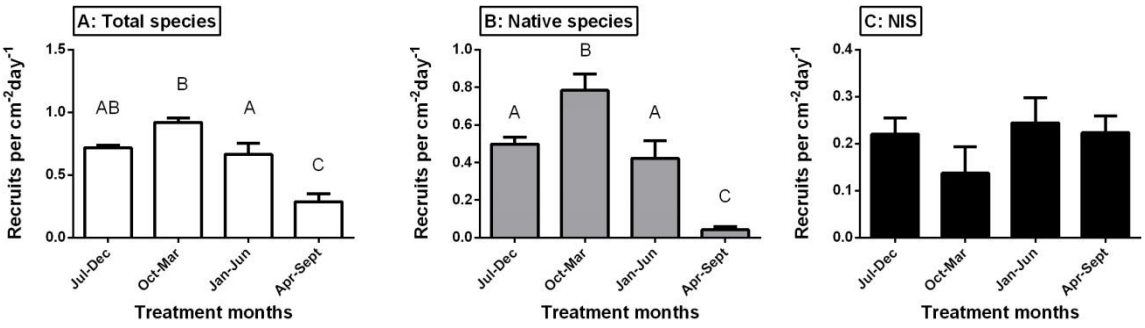

Figure 3.24: Recruitment of sessile and sedentary species for the 6-month settlement treatment for the various species grouping (+SE, N=10), when: A) All species; B) Native species; and C) NIS species. Note: Letters represent significant differences between groups; white denotes all species, grey denotes native species and black denotes NIS.

3.3.2.6 Recruitment/cover of individual species on 6-month treatments

At a species level the solitary ascidian *Molgula ficus* was a dominant species for three of the four deployment periods for the 6-month treatments: Jul-Dec, Oct-Mar and Jan-Jun, contributing to a majority of space occupied (42% ± 4.7, 83% ± 8.3, and 66% ± 8.0 respectively; Figure 3.24 and 3.25). There was a significant difference in the recruitment of individual species for all of the 6-month treatments ($H_{[17]}$=85.29, $p < 0.0001$, $H_{[6]}$=45.29, $p < 0.0001$, $H_{[6]}$=38.08, $p < 0.0001$and $H_{[13]}$=35.96, $p = 0.0007$, respectively; Figure 3.24A and B; and 3.25A and B).

Molgula ficus occupied significantly more space than five of the NIS and six of the native species for the Jul-Dec treatment (Figure 3.24A); all species except *Ciona intestinalis* for Oct-Mar (Figure 3.24B); and all species except *Pomatoceros taeniatus* in Jan-June (Figure 3.25A). The only 6-month deployment period where *Molgula ficus* was not a dominant species was in April to September (austral winter; Figure 3.25B). For this deployment period the NIS bryozoan *Bowerbankia gracilis* occupied significantly more space than three native species and one NIS. In addition to this, the native bryozoan *Celleporaria foliata* had significantly greater space occupancy than three of the native species for the Jul-Dec treatment; *Ciona intestinalis* had significantly greater cover than the one native and one NIS in Oct-Mar; and *Eudendrium capillare* had significantly greater cover than the one native and one NIS in Jan-Jun (Dunn's Appendix C, Tables 19-22).

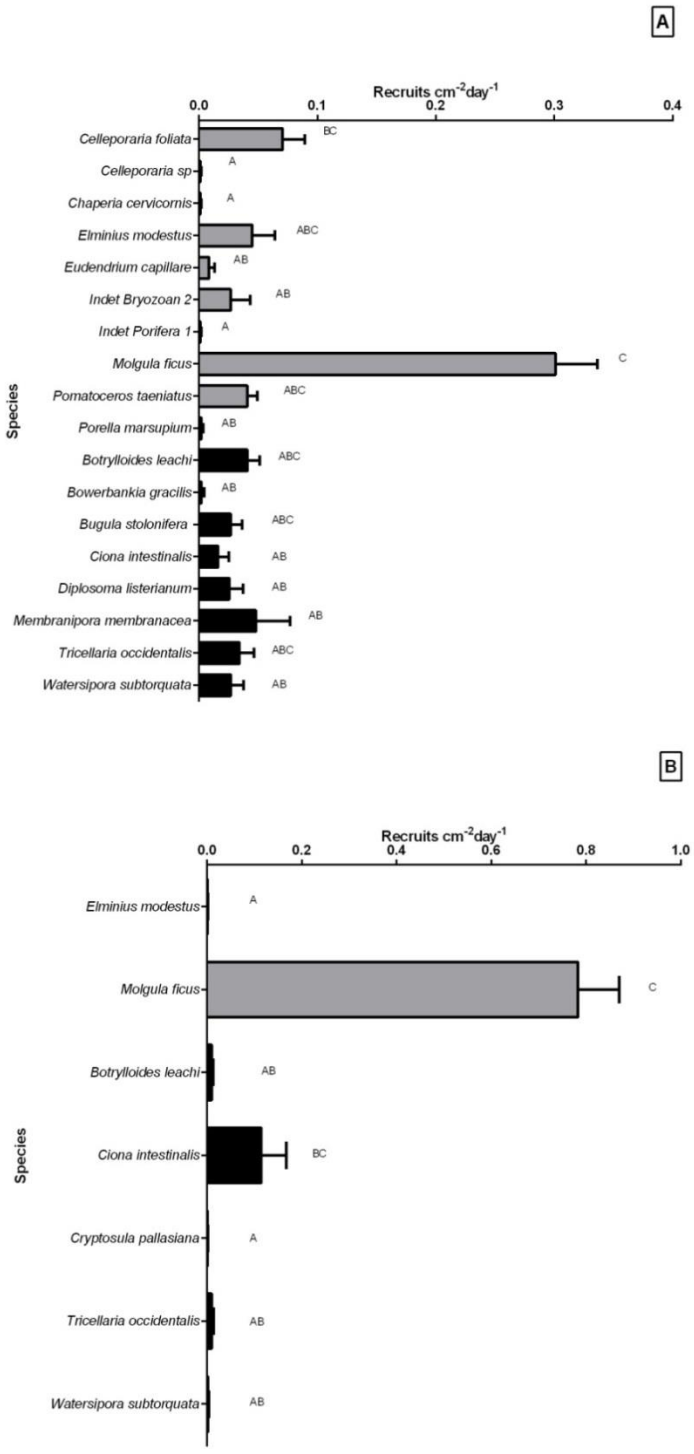

Figure 3.25: Recruitment of individual native species and NIS (+SE, N=10), during the 6-month treatments for four different seasons: A) July-December; and B) October-March. Note: Grey = native species, Black = NIS

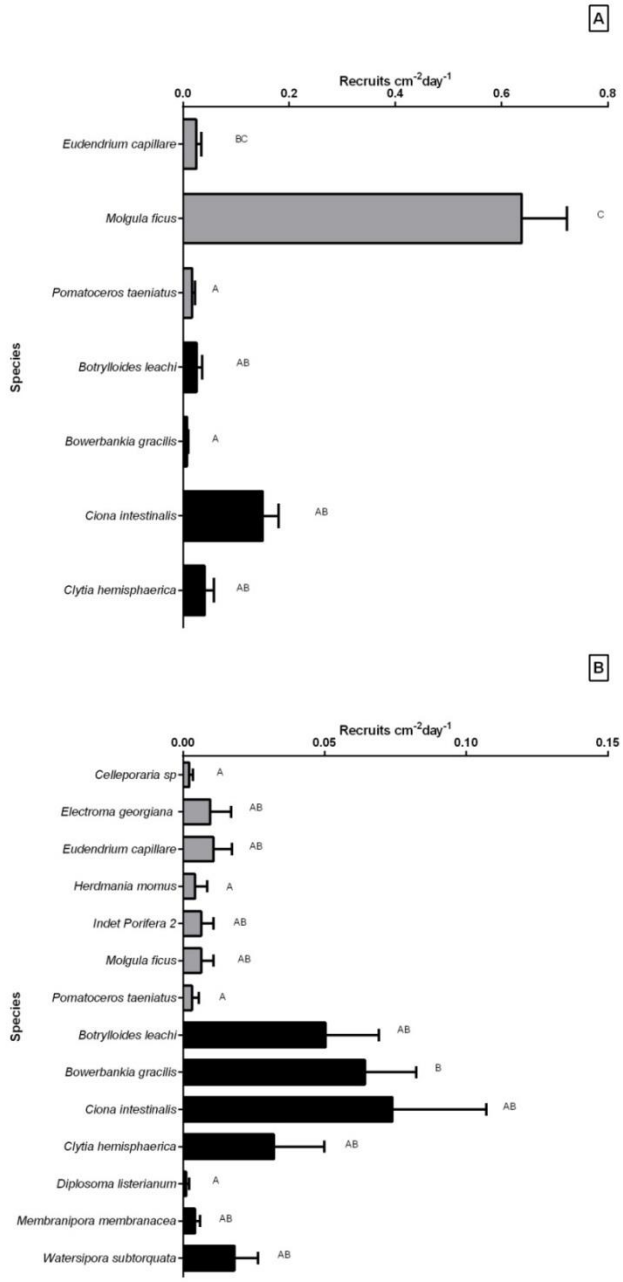

Figure 3.26: Recruitment of individual native species and NIS (+SE, N=10), during the 6-month treatments for four different seasons: A) Jan-Jun and B) Apr-Sep

3.3.2.4 Recruitment/cover of native versus NIS on 6-month treatments

Combined native species recruitment/growth was significantly greater than NIS recruitment/growth for Jul-Dec, Oct-Mar and Apr-Sep treatments ($t_{[18]} = 5.633$, $p < 0.0001$; $t_{[18]} = 6.285$, $p < 0.0001$; and $t_{[18]} = 5.024$, $p < 0.0001$ respectively; Figure 3.26). The recruitment on the Jan-Jun treatment, which spanned the recruitment period where *Molgula ficus* was not present, was also significantly different between native species and NIS ($t_{[18]} = 1.618$, $p = 0.1230$); however, NIS settlement was significantly greater than native species settlement for this period.

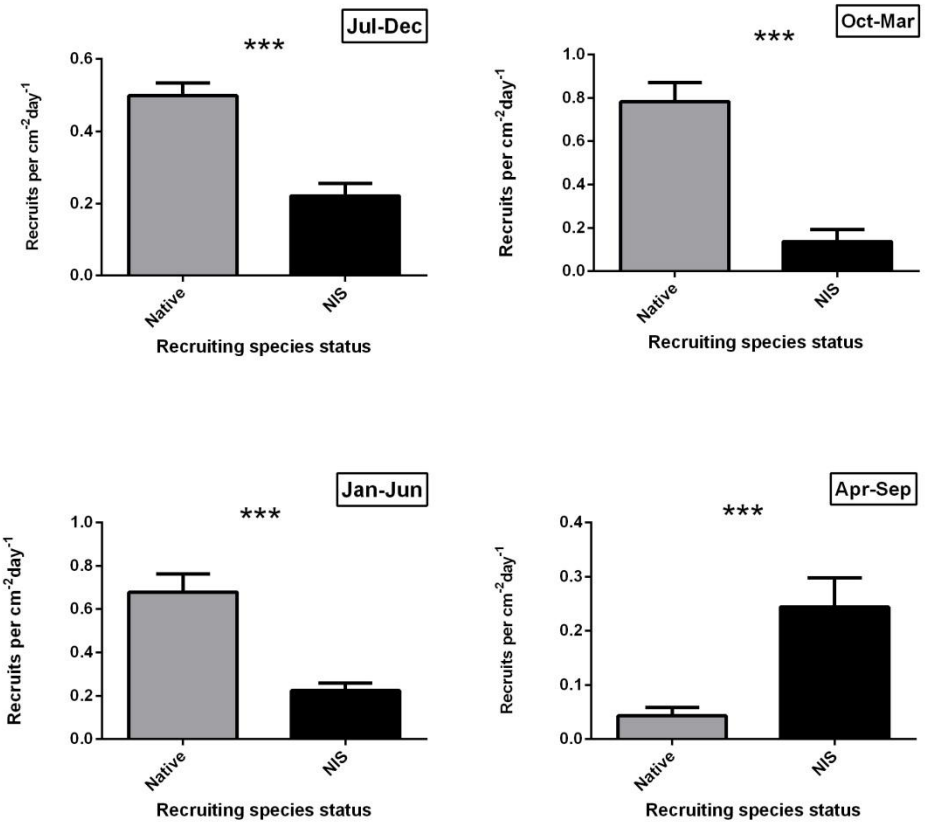

Figure 3.27: Recruitment of combined native and NIS species across 6-month treatments (+SE, N=10). Note: *** above columns represent significant differences between these variables.

3.3.2.5 Unoccupied space

Percent bare space cover for 3 month treatments was considerably lower than 6 month treatments. There was a significant difference in the percent cover for both the 3 and the 6 month treatments ($F_{[17,36]}$= 43.54, $p < 0.0001$, $F_{[3,36]}$= 5.856, $p < 0.0023$, respectively; Figure 3.27A and B; Tukeys Appendix C, Tables 23). Treatments July-Sep and Apr-June had significantly greater bare space than Oct-Dec and Jan-Mar three month treatments. Moreover 6 month Jul-Dec treatment had significantly greater bare space than Oct-Mar and 6 month treatment Apr-Sep had significantly greater bare space than both Oct-Mar and Jan-Jun.

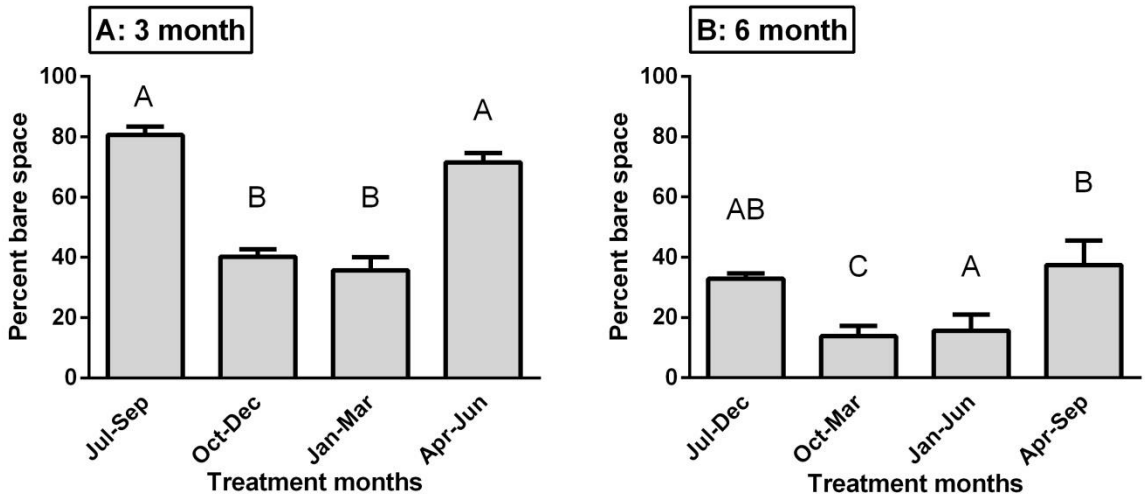

Figure 3.28. Unoccupied bare space calculated for different treatments (+SE, N=10). A) 3 month treatments and B) 6 month treatments. Note: Letters represent significant differences between groups.

3.4 Discussion

This chapter aimed to illustrate differences in the recruitment of native and NIS sessile invertebrates, while simultaneously examining differential growth and community composition of native and NIS as a response to different seasonal and time based deployments (3 and 6- months), a number of generic patterns were evident. Recruitment generally takes place in austral late spring to early autumn, although some species still recruit in the winter months. Moreover NIS generally recruited at greater densities and for longer periods than native species.

In this chapter I hypothesised that; there will be a difference in the recruitment densities of native and NIS (H4). NIS observed within this study recruited for longer periods and at higher density than native species (Table 3.2). NIS recruited at significantly higher numbers than natives for the eight month period October through to May, spanning the majority of spring and all of summer and autumn (Figure 3.16). Numerous NIS repeatedly contributed heavily towards the calculated significant differences seen for individual months. Reoccurring dominant NIS recorded monthly included: the bryozoans *Tricellaria occidentalis*, *Bugula stolonifera*, *Watersipora subtorquata* and *Bowerbankia gracilis*; the chordates *Botrylloides leachi* and *Ciona intestinalis*; and the cnidarian *Obelia geniculata*. Furthermore, all of the previously mentioned species that recruited in high numbers also recruited for at least five months (most of them for longer periods).

Native species displayed significantly greater recruitment numbers than NIS for two months of the sampling periods: June and August (winter) (Figure 3.16). This result was dominated by the increased settlement of one species, the hydroid *Eudendrium capillare*,

which is a known cosmopolitan species (Huisman et al., 2008). Annual recruitment of hydroids has been described as a response to environmental cues such as solar radiation (irradiance), salinity and temperature (Gili and Hughes, 1996). Responding to environmental cues results in inconsistent recruitment as species recruit only in years when conditions are correct. This effect is considered to be especially true in temperate waters (Di Camillo et al., 2008). Results in this chapter support the hypothesis that there will be differences in recruitment between native and NIS, thus I accept the hypothesis.

Quantity and quality of recruiting larvae are generally considered important factors that facilitate invasion success (Williamson and Fitter, 1996). Moreover the probability of success is increased with increased frequency of inoculation(s) (Drake, 1991; Verling et al., 2005). NIS within the present study recruited for an average of 4.7 months whereas natives recruited for an average of 2.6 month. The two species with the longest recruitment period were the NIS ascidians *Ciona intestinalis* (solitary) and *Botrylloides leachi* (colonial) (both recruited for 10 months) and were absent only during the central winter months (July and August). Notably, these two species also had higher recruitment compared to other species both native and NIS within the same months. Recruitment in July, which falls in the middle of Austral winter, was very low with only two species recorded recruiting onto settlement plates. Environmental parameters are highly variable in littoral ecosystem (Coma et al., 2000), this is especially evident in temperate environments (Clarke A, 1988). Studies that focus on seasonal variations in species recruitment generally show patterns of high species productivity of most taxa in spring and summer, this however decreases through autumn and reaches a minimum in winter where some species become dormant (Coma et al., 2000).

Reasons behind the seasonality in production/growth are usually linked to temperature (Clarke A, 1993; Coma et al., 2000).

In a propagule pressure context, NIS observed within this study were generally characterised by high numbers of individuals that are available to settle across longer periods (i.e., their high numbers and duration of presence in the environment led to longer recruitment periods) thus, the NIS are able to swamp the environment. These results are similar to the theories that suggest that the probability of a new introduction increases with the size and frequency of release of a new species (Underwood and Fairweather, 1989; Drake and Lodge, 2004). Moreover, a similar theory of supply-side ecology recognises that varying densities of larvae contribute to size and species composition of marine assemblages (Hughes et al., 2000).

Species richness and recruitment rates recorded within this study were generally low on individual settlement plates. Although individual species or colony size was not recorded during recruitment observations it was personally observed that space was generally not a limiting resource and as such interference competition from previous recruits is not believed to strongly influence recruitment. Over the span of the sampling year, 50 species were recorded on the artificial bare substrate that was made available for one month, at a ratio of ~1.6:1 natives to NIS (Table 3.2). Although overall native species richness was 1.6 times greater than NIS, the number of NIS recruits was significantly greater than that of the native recruits for the majority of the observed year (Figure 3.16).

The second hypothesis in this chapter stated; space occupied and species composition of 3 and 6-month treatments will be a function of recruitment (H5). Differences between one

month recruitment and six month treatments were considerable. Monthly recruitment was characterised by significantly greater NIS recruitment for 10 months of the year, while six month treatments were characterised by significantly greater recruitment of native species for three of the four different temporal treatments, thus the hypothesis is rejected. Therefore, it appears that species composition and densities here are not a function of recruitment. This result superficially lends support to previous research that indicates that biotic factors, such as competition (Jackson, 1977), predation (Connell, 1961) and species interactions (Buss, 1979), are what influences benthic community assemblages.

Observations of 6-month settlement plates show that recruitment numbers were not the dominant factor regulating species composition on bare space within the studied assemblages (Figure 3.26). The native solitary ascidian *Molgula ficus*, a known invader to the Northeast Pacific (Lambert, 2007), was a dominant species on all 6-month treatments, where recruitment was recorded for the same months. Solitary ascidians are not thought to be susceptible to overgrowth competition (Claar et al., 2011), and some species have been shown to grow rapidly (Lambert, 1968). Ascidians observed within this research certainly seemed unaffected by competitors; individuals reached a large size (width up to 50mm) within 3 months, and showed gregarious settlement, reducing space and smothering competitors.

Factors such as fecundity, life history and competitive ability differ between colonial and solitary modes of life (Jackson, 1977). The results in this chapter contradict others that have found some solitary organisms, although numerous, occupied little space. Yet, in the experiments undertaken here the 6-month assemblages were dominated by the native solitary

ascidian, *Molgula ficus*, followed by the also solitary NIS ascidian *Ciona intestinalis*. Observations made within the present study however are similar to those of Miller and Etter (2008) who showed increased abundances of the solitary ascidian *Molgula citrina* on horizontal substrates, which was attributed to a shading effect in their study. Similarly, these researchers found that *M. citrina* impacted on the abundance of other species (Miller and Etter, 2008).

Studies have shown that bryozoan colonies can make dominant contributions to biomass within communities (Goren, 1979; Bailey-Brock, 1989). However in this study, the bryozoans recorded occupied minimal space. Of interest is that the bricks that provided stability to the plates did have substantially more bryozoans present, with the holes of the bricks often fully encrusted (pers. obs.). This suggests that the bricks were better suited substrates for these species than the PVC settlement panels. This may be due to a number of factors such as substrate granularity (roughness), rugosity creating micro-habitats and chemical composition of the different substrates (Brewer, 1984).

Abiotic environmental conditions such as turbidity, solar irradiation and salinity are thought to be limiting factors behind seasonality of benthic invertebrate community composition (Gili and Hughes, 1996; Di Camillo et al., 2008). These abiotic conditions are said to drive phytoplankton cycles (Coma et al., 2000), which are a major biological trigger for many benthic invertebrates (Di Camillo et al., 2008). Although succession was not the focus of this work, my observations of species composition and post-recruitment success can be evaluated as such. Previous research illustrates the importance of the time of year and season in which settlement plates were deployed (Underwood and Anderson, 1994). The

results in this chapter support this to an extent, as individual species showed differing dominance between monthly and 3-month treatments. However, observations on 6-month treatments were in contradiction, as the native solitary species *Molgula ficus* became the dominant space occupier in all but one treatment regardless of season/timing of deployment, for reasons which may include growth rate and the ability to outcompete competitors.

NIS within this study recruited at much greater densities than native species (Figures 3.4-3.15). Characteristics of the 3-month treatments complemented recruitment data, with NIS showing dominance in seasons when recruitment was high. Six month treatments however, did not reflect recruitment success observed on monthly plates (Figures 3.24 and 3.25). Regardless of recruitment numbers, NIS did not show an increase in space occupancy. This observation is particularly pertinent as it suggests that propagule pressure may not swamp native species in this study, but instead some other factor(s) is at play. Understanding how NIS utilise space and what factors facilitates their success is important to predict and mitigate impacts of NIS (Carlton, 2001a). The space limited assemblages with dominant native competitors created within this study offer a unique opportunity to elucidate how NIS co-exist in highly competitive resource limited communities. Recruitment of offspring is an important step in the survival of individuals/ species and as such is a crucial step in understanding epibiosis, as such this chapter has provided background information for Chapter 4.

CHAPTER 4.
EPIBIOTIC PRESSURE AND PREFFERENCE

4.1 Introduction

Community ecology advocates that the most important factor that determines the relative abundance of individual species within an assemblage, as well as the sequence of species assembly, is the ability for each participating species to compete (Jackson, 1977). A species' competitive ability has also been shown to play a key role in NIS success (Baker et al., 1965; Callaway and Ridenour, 2004), however many factors behind the success of benthic sessile NIS still remain unclear. Recruitment sequence leading to priority effects have been shown to provide enhanced competitive status to early recruits (Wilbur and Alford, 1985). The recruitment of NIS recorded within Chapter 3 was generally higher and for longer periods of time than recruitment of native species. However, the results of longer term assemblage development revealed that, regardless of recruitment pressure, NIS did not maintain dominance after six months, regardless of deployment period. This suggests that recruitment effects alone do not predict competition outcomes.

Competition between benthic invertebrates is generally explained by two types of competition: interference competition, when one competitor directly impacts another competitor (Case and Gilpin, 1974; Jackson, 1977; Menge, 1995); and exploitative competition, when one competitor's utilisation of a resource diminishes the use of the same or a different resource for another organism (León and Tumpson, 1975; Wilson, 1990; Menge, 1995; Ferguson et al., 2013). Within a benthic marine assemblage context, a greater emphasis has been placed on interference competition over exploitative competition (Hart

and Marshall, 2011), with many works illustrating that interference competition is intense in space limited environments and as such is an important factor in regulating establishment (Connell 1961; Jackson 1977; Buss 1979). Lending the view that for a NIS to become successful and established where resource availability is low it must appropriate resources from competitors via interference competition or be able to successfully survive off the limited resource (Tilman, 1982; Hart and Marshall, 2011).

Benthic assemblages are generally dominated by solitary and colonial sessile species (Jackson, 1977; Buss, 1990), commonly with a filter feeding regime, which is energetically advantageous. However, the lack of locomotion does subject these species to an array of competitive pressures (Harder 2009) as they have limited escape capacity. In this context, space is the key limited resource that results in constant interference competition encompassing interactions such as overgrowth, undercutting and epibiosis (Buss, 1979).

Recruiting species faced with a myriad of factor that affects their success. The presence of existing species can greatly influence the survival of not only recruits but also affect post recruitment success. The "Priority effect" occurs when one or more species early arrival within an assemblage affects the success (establishment, growth or reproduction) of a later arriving species (Wilbur and Alford, 1985; Fukami, 2004; Von Gillhaussen et al., 2014). Priority affect can lead to lasting changes in an individual species or species composition within an assemblage (Chase, 2003; Von Gillhaussen et al., 2014). Individuals already present on a substrate have the potential to directly reduce settlement of new individuals by predation on larvae (Cowden et al., 1984; Osman et al., 1989), and limiting substrate space availability (Stebbing, 1972; Osman, 1977) or alternatively facilitate settlement by providing

biogenic substrate (Wahl and Lafargue, 1990; Wahl and Mark, 1999). Moreover, once new individuals are settled, resident species may still influence the success through predation and/ or overgrowth (Osman, 1977).

Overgrowth competition is a strong regulatory force that influences the density and distribution of species within benthic encrusting assemblages (Gordon, 1972; Jackson, 1977; Buss, 1979; Jackson, 1979), often resulting in mortality for the underlying competitor (Jackson, 1979; Russ, 1982). A species' ability and/or strategy of avoiding overgrowth generally focuses on that species' defence mechanisms (Jackson, 1977; Bruno and Witman, 1996). Prime examples of these include chemical defence (Wahl et al., 1994), the presence of antifouling surfaces (Davis et al., 1989) or spines (Wahl, 1989) as touched upon in Chapter 1.

Undercutting is a process where a competing species quickly grows under the edge of another, ultimately dislodging the competing species. Undercutting is generally used to describe barnacle competitive strategy (*sensu* Connell 1961). Epibiosis-like overgrowth is ubiquitous, with very few living substrates within benthic assemblages being un-colonisable (Wahl, 1989). There is a growing and robust body of evidence as to the consequences of epibiosis (see Chapter 1), with impact affecting species differently depending on numerous variables, such as the mode of life, morphological characteristics and/or defensive ability (Wahl, 1989). The impacts of epibiosis are not exclusively negative for the underlying competitor, also known as basibiont. It has been documented that this association may play a role in protection from predators (Christophersen, 1985; Barkai and McQuaid, 1988) and may also increase the availability of nutrients (Wahl, 1989). As mentioned in Chapter 1, the negative impacts caused by epibionts include reduced water motion and gas exchange,

competition for food and blocking light/nutrients to name a few (Wahl, 1989; Wahl and Hay, 1995; Harder, 2009). Much like overgrowth competition, epibiosis often results in the mortality of the basibiont. This is considered especially true for benthic sessile organisms that often require their outer surfaces for processes such as nutrient and waste exchange (Harder, 2009).

The consequences of an epibiont/basibiont association go both ways, with positive and negative implications to epibionts. Epibionts (individuals or colonies) are often reliant on the stability of the basibiont. Hence, factors such as natural mortality, disturbances or predation experienced by the basibiont can significantly impact upon epibiont success (Harder, 2009). However, the benefits of living as an epibiont outweigh the negative, which is apparently evident given this mode of life's prevalence in the environment (Russ, 1982; Wahl, 2010).

Adequate bare substrate to settle upon is considered one of the most limited of resources for sessile marine invertebrates (Connell, 1961; Paine, 1966; Dayton, 1971; Paine, 1974). As unoccupied space becomes increasingly rare, new recruits must adapt to an epibiotic mode of life (Wahl and Mark, 1999). Moreover epibiosis also supports life of some benthic sessile species in areas where they could not normally colonise, such as soft sediment substrates (Schejter and Bremec, 2007; Schejter et al., 2011). A similar phenomenon has been used to describe the range expansion of NIS, where species use living substrates (basibionts) as stepping stones to move across barriers that they would normally be unable to transcend (Ricciardi, 2001).

A reduction in fouling pressure from overgrowth or epibiosis may also result in greater fitness. A species that lacks fouling pressure may theoretically reallocate resources originally utilised for defence to other functions, such as increasing biomass and reproductive capability (Bossdorf et al., 2004). Moreover, it has been suggested that settlement as an epibiont may not only reduce the need to find suitable un-colonised substrate but may also release the species from overgrowth pressure (Wahl, 1989).

The outer surfaces of marine benthic invertebrates are generally subjected to intense fouling pressure, especially on hard substrate where adequate settlement substrate is a limited resource (Jackson and Buss, 1975). When a species remains devoid of epibionts in the presence of potential settlers, it is considered that the species has some mechanism of protection (Harder, 2009). Defence mechanisms generally involve morphological adaptions (in the form of antifouling defence adaptions) (Feifarek, 1987) or chemical antifouling (Davis and Wright, 1989). With this myriad of negative and positive gains being present in epibiont/basibiont associations, it can be assumed that there is some degree of co-evolution between epibiont and basibiont associations. Yet, very few works have focused on this aspect as it appears difficult or impossible to detect (Galle and Parsley, 2005).

As previously mentioned, overgrowth competition acts as a function for regulating certain species densities within assemblages. However, it has been suggested that epibionts are not subjected to the same overgrowth pressure as species that occupy bare substrate (Jackson, 1977). The function of epibiosis in the success of NIS establishment, and ultimately invasion success, has largely been unexplored. Therefore, this study aims to explore the potential differences between native and NIS epibiotic settlement strategies by observing

settlement onto experimental recruitment substrates and comparing this to assemblages of varying ages on the same experimental substrates. Additionally, this chapter aims to discover differences in settlement onto different basibionts species, distinguishing these as being either native or NIS. Specifically, I hypothesise that:

H6: The frequency of settlement onto native basibionts will be significantly greater than the settlement frequency onto NIS species;

H7: Native epibionts will show preference to settle onto bare space over settlement onto either native or NIS species;

H8: NIS ratio settlement of basibiont compared to bare space will be greater for 6-month treatments compared to 3-month treatments

From the results of this study, I discuss potential advantages NIS have within their invaded ranges over natives, with regards to competition for space and the deleterious effect of epibiosis.

4.2 Methods

Details of the location where samples were collected are provided in Chapter 3 (see section 3.2.1). Similarly, information on the calculation of recruitment and space occupancy were described in Chapter 3 (section 3.2.3) and hence I refer the reader to those sections for that information. Settlement plates (see Chapter 3 for the set-up and deployment methods for the plates) were used to test the three hypotheses in this chapter.

4.2.1 Epibiosis analysis

Following determination of primary space settlement, as described in Chapter 3 (section 3.2.4), all species that occupied primary space were analysed to determine if they had any epibionts. This involved removing each individual organism and examining it under a dissection microscope. All individuals that had epibionts were identified to lowest taxonomic unit (LTU) (see to Chapter 3, section 3.2.3), and given a unique identification number. Each individual epibiont on identified basibionts was counted, identified to LTU, recorded and assigned a unique identification number.

Epibiotic pressure is discussed within this thesis as generally having negative impacts (*sensu* Harder, 2008) on the basibiont thus reducing competitive ability. Research regarding epibionts onto the tough outer tunicas of ascidian is uncommon, and impacts onto *Molgula ficus* possibly non-existent. However, research by Claar (2011) do show little susceptibility to overgrowth competition for a different ascidia (*Ascidia ceratodes*). These authors suggest that the growth of epibionts onto the thick tunica of *Ascidia ceratodes* has minimal impacts unless the overgrowth covers the syphons. Similar to this, it was observed during this study that epibionts on the tough outer tunica of *Molgula ficus* did not seem to affect fitness, with this species becoming dominant on a majority of 3 and 6 month settlement plates. This study aimed to illustrate differences in epibiosis between native and NIS species, considering that adverse effects of epibiosis outweigh benefits. Due to the prevalence of epibionts on *Molgula ficus* an additional suite of analyses were conducted with *Molgula ficus* omitted.

4.2.2 Statistical analysis

Differences in overall settlement on native and NIS was analysed using a chi-square goodness-of-fit test. To determine whether counts of epibiosis on native or NIS departed from the expected ratio of 1:1, a chi-square test for association was conducted between epibiont status (native/NIS) and preference for settling on native or NIS basibionts for the 3-month and 6-month settlement treatments.

The frequency of settlement of native or NIS epibionts recorded attached to native and NIS basibionts was compared using the non-parametric Kruskal-Wallis with Dunns procedures, or Mann-Whitney U tests when only two unpaired groups were present. Pairs were allocated into four groups depicting their epibiont/basibiont status:

- NIS/NIS;
- NIS/native;
- native/NIS; and
- native/native.

The differences between settlement of native and NIS as epibionts and settlement onto bare space were examined using the ratio of settlement on basibionts versus the recruitment onto bare space for the same treatment. Ratio settlement was calculated by taking an individual species recruitment onto basibionts (individuals $cm^{-2}day\text{-}^{1}$) and dividing it by the same species background recruitment (individuals $cm^{-2}day\text{-}^{1}$) onto bare settlement plates sampled monthly for the same duration /treatment time. Data was log transformed to aid in the visual presentation of figures. This allowed for settlement on basibionts to be above the x axis and settlement onto bare space under the x axis. Ratios > 0 indicate increased settlement

onto basibionts (e.g. ratio=2 means that the settlement onto basibionts was 2 times higher than the settlement on background bare space settlement); ratios = 0 indicate equal settlement on basibionts and bare space; and ratios < 0 indicate a higher settlement onto background bare space settlement (see Figure 4.1 for hypothetical example showing calculated ratio settlement)

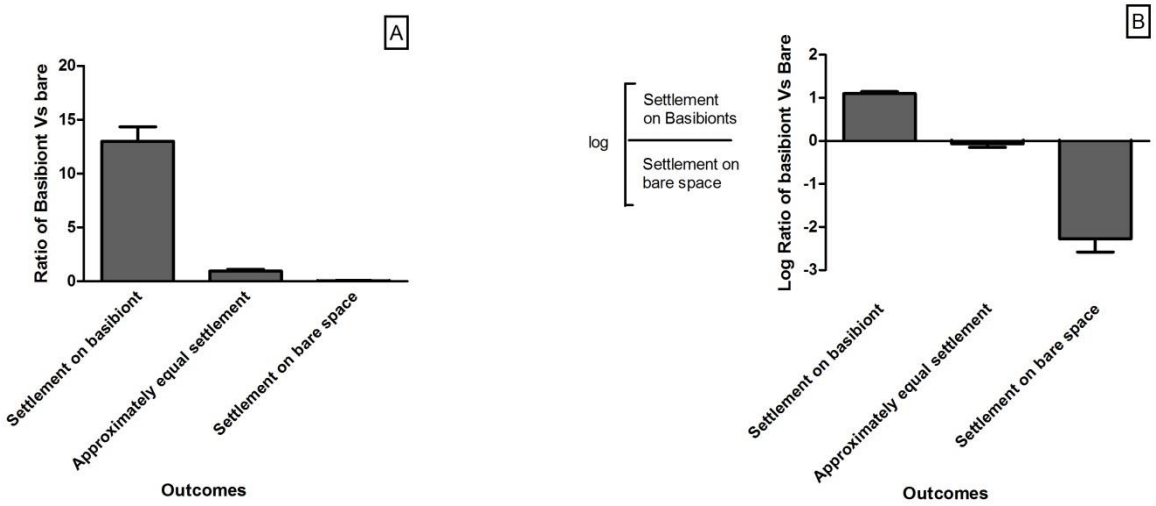

Figure 4.1: Hypothetical example to demonstrate presentation of the ratio settlement between basibionts and bare space. A) Ratio settlement ; >1 = increased settlement on basibiont; ≈0.5 = equal settlement on both basibiont and bare space; close to 0 = settlement on bare space. B) Log transformed ratio settlement (used in chapter) ; > 0 = greater settlement on basibiont, 0 = approximately equal settlement on basibiont and bare space, and < 0 = higher settlement on bare space.

Ratio settlement for each of the epibionts for the 3-month and 6-month treatments was examined to determine differences in settlement choice displayed by the different species of epibionts. Additionally, species were grouped according to their native/NIS status as well as grouping epibionts into their four groups depending on the epibiont/basibiont association.

Data were analysed using a One-way ANOVA with Tukey's post-hoc analysis, or the non-parametric tests Kruskal-Wallis, with Dunns procedures when the assumption of normality was violated. An unpaired t-test, or the non-parametric equivalent Mann-Whitney U test, was used when only two independent variables existed.

As stated above a suite of analyses were conducted that omitted *Molgula ficus* because of the prevalence of epibionts on *Molgula ficus* and the fact that epibiotic settlement on this species may seems to have no impact on its fitness (personal observation). Within this thesis epibiotic pressure is discussed as generally having negative impacts on the basibiont, thus reducing competitive ability, hence it was found fitting to factor in the removal of *Molgula ficus*.

4.3 Results

4.3.1 Three and six month settlement treatments

For 3-month treatments, 2186 individual recruits were recorded settling onto native species, or 175 with *Molgula ficus* omitted as a basibiont. Simultaneously, 53 individual recruits were recorded settling onto NIS. Settlement frequencies onto native species or NIS differed significantly with and without *Molgula ficus* as a basibiont ($\chi^2_{[1]} = 2032.018$, $p < 0.0001$ and $\chi^2_{[1]} = 65.281$, $p < 0.0001$, respectively; Figure 4.1A and B), with settlement onto native species being ~ 41 fold greater than settlement onto NIS with *M. ficus* and ~3.5 fold without *M. ficus*.

Almost 2000 (1952) recruits settled onto native species in the 6-month treatments, with 247 recruits settling when *M. ficus* was absent, and 54 individual recruits settled on to

NIS. Similar to the 3-month treatments, the 6-month treatments also departed from the expected ratio with and without *M. ficus* included ($\chi^2_{[1]}$ = 1795.815, p <0.0001 and $\chi^2_{[1]}$ = 123.751, p <0.0001, respectively; Figure 4.1C and D), with settlement on native species more than 35 times higher than settlement onto NIS when *M. ficus* was included. When *M. ficus* was excluded as a basibiont settlement was ~4 times greater.

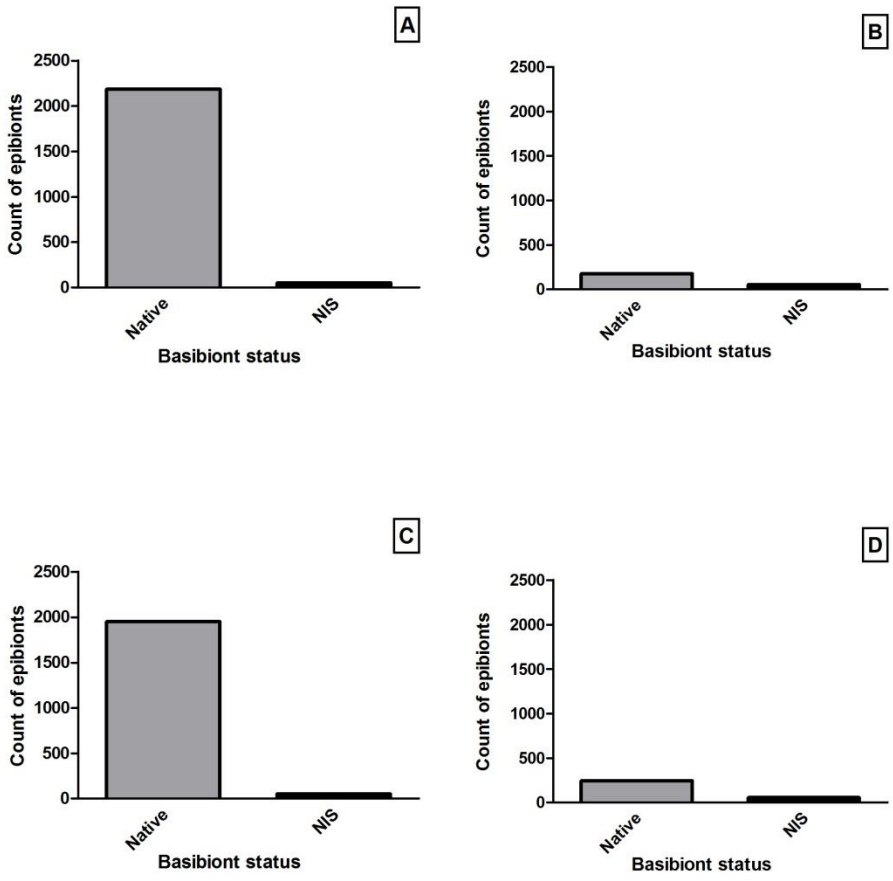

Figure 4.2. Total frequency of all epibionts settling on native and NIS basibionts for the settlement treatments of: A) 3-months with *Molgula ficus* present; B) 3-months without *Molgula ficus* present; C) 6-months with *Molgula ficus* present; and D) 6-months without Molgula ficus.

There was a statistically significant association between epibiont status and basibiont status for the 3-month treatments when the basibiont *M. ficus* was present as substrate ($\chi^2_{[1]}$ = 3.965, p = 0.046; Figure 4.2A). In this instance, native epibionts were less likely to settle on NIS basibionts than natives (i.e., native tended to settle on natives), while NIS epibionts showed a greater tendency to settle on NIS than natives. In contrast, there was no statistically significant pattern in the 3-month treatments when *M. ficus* was excluded, or in the 6-month treatments with and without the inclusion of the basibiont *M. ficus* ($\chi^2_{[1]}$ = 1.220 , p = 0.269, $\chi^2_{[1]}$ = 0.155 , p 0.693 and $\chi^2_{[1]}$ = 1.205 , p = 0.272, respectively; Figure 4.2B, C and D).

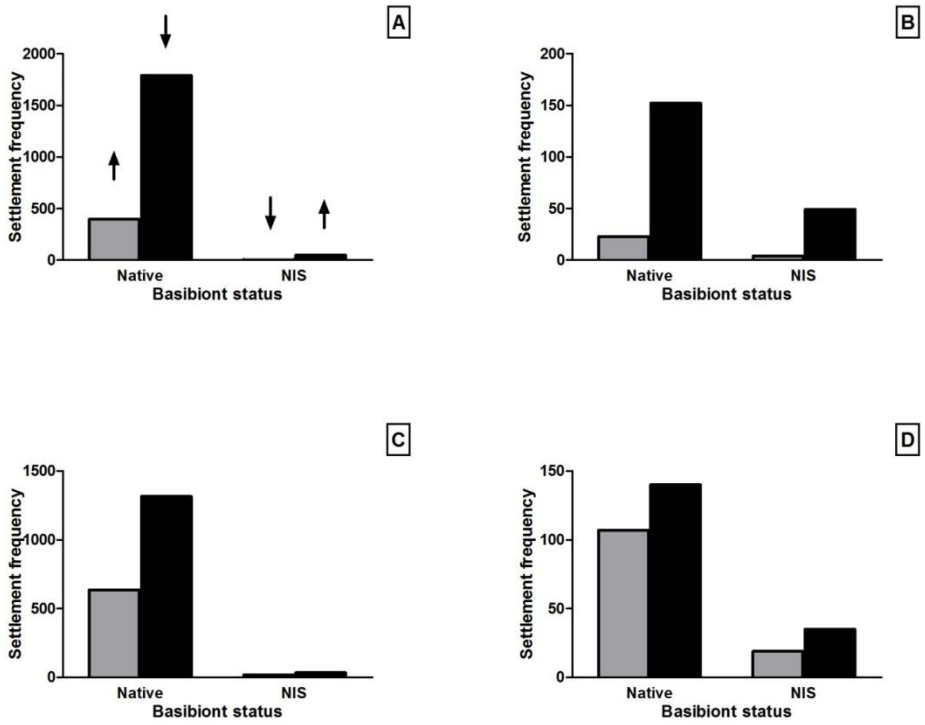

Figure 4.3. Total settlement frequency of native and NIS epibionts on native and NIS basibionts for the settlement treatments of: A) 3-month treatment; B) 3-month treatment with *Molgula ficus* omitted; C) 6-month treatment; and D) 6-month treatment with *Molgula ficus* omitted. Note: Arrows represent increased or decreased recruitment from what would be expected. Grey bars represent native species and black NIS

4.3.1.1 Seasonal influence 3-month treatments

For the 3-month treatment deployed from Jul-Sep, the only epibionts/basibiont association observed was native epibiotic settlement on native basibionts. These frequencies of settlement were observed to be the same with or without the presence of the basibiont *M. ficus* (Figure 4.3A and B). No native species settled on NIS during the 3-month treatment that occurred from Oct-Dec. Statistical analyses showed that NIS epibionts settled on native basibionts at significantly higher frequencies than native epibionts on natives basibionts, or NIS epibionts on NIS basibionts ($H_{[2]}$=24.87, p< 0.0001; Figure 4.3C). The same treatment with *M. ficus* omitted also showed significant differences ($H_{[2]}$=9.105, p =0.0105; Figure 4.3D; Dunn's Appendix D, Table 1). However, with *Molgula ficus* omitted both NIS/native and NIS/NIS epibionts/basibiont associations had significantly higher frequencies than the native/native association.

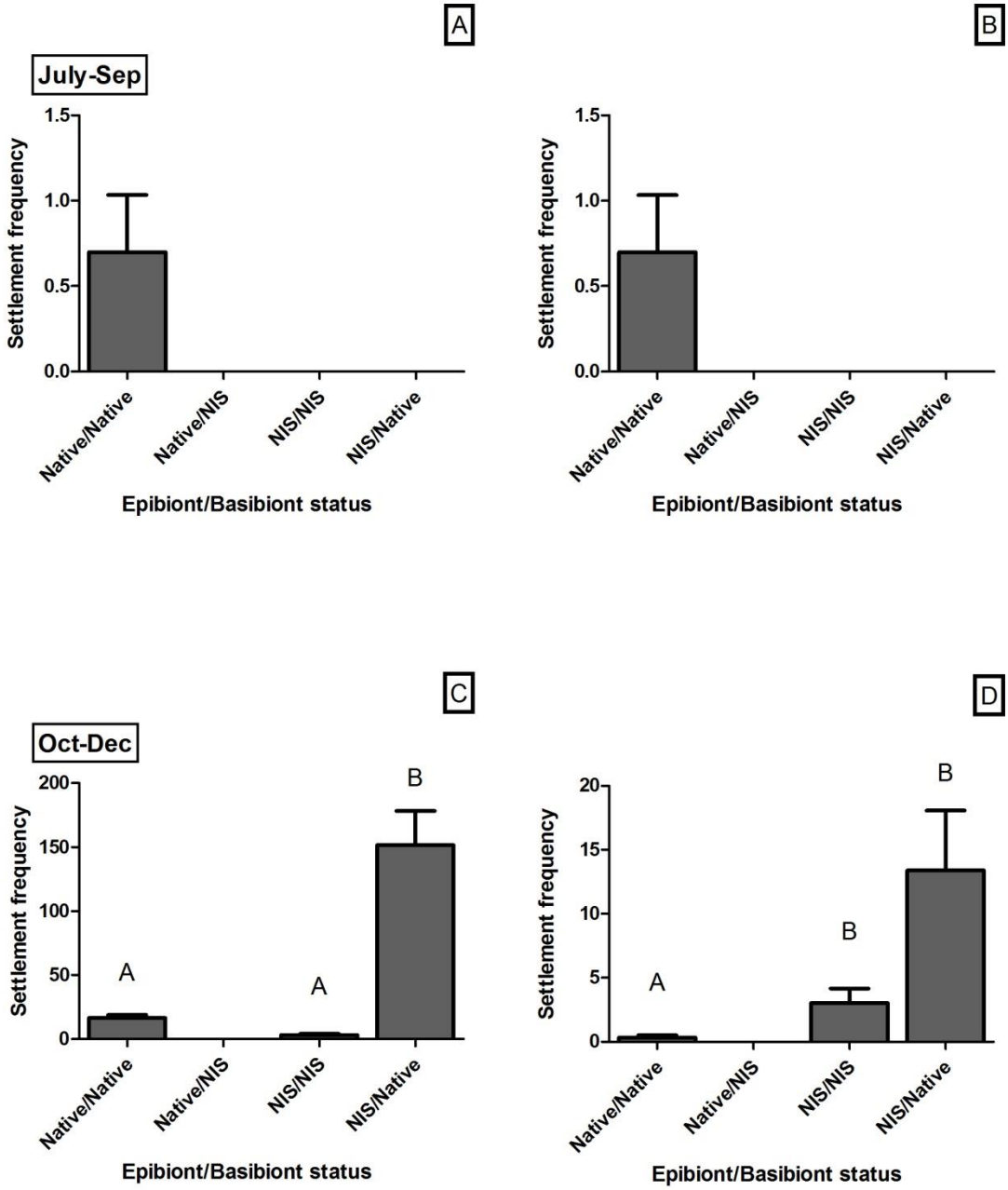

Figure 4.4 Settlement frequency of native/NIS epibiotic settlement on native/NIS basibionts across 3-month treatments during four settlement periods (+SE), when: A) Jul-Sep with *Molgula ficus* present; B) Jul-Sep without *Molgula ficus* present; C) Oct-Dec with *Molgula ficus* present; and D) Oct-Dec without Molgula ficus. Note: letters denote significant differences.

Settlement frequencies between the different epibionts/basibiont associations for the Jan-Mar sampling period differed significantly ($H_{[3]}$=27.57, $p < 0.0001$; Figure 4.4A), with frequencies of native/native and NIS/native being significantly greater than that of native/NIS and NIS/NIS associations. There was no significant difference for the same treatment and treatment period when *M. ficus* was omitted ($H_{[3]}$=27.57, $p < 0.0001$; Figure 4.4B). During the 3-month treatment of Apr-Jun the only epibionts/basibiont association observed was NIS epibionts settling on NIS basibionts (Figure 4.4C and D) (Dunn's Appendix D, Table 1).

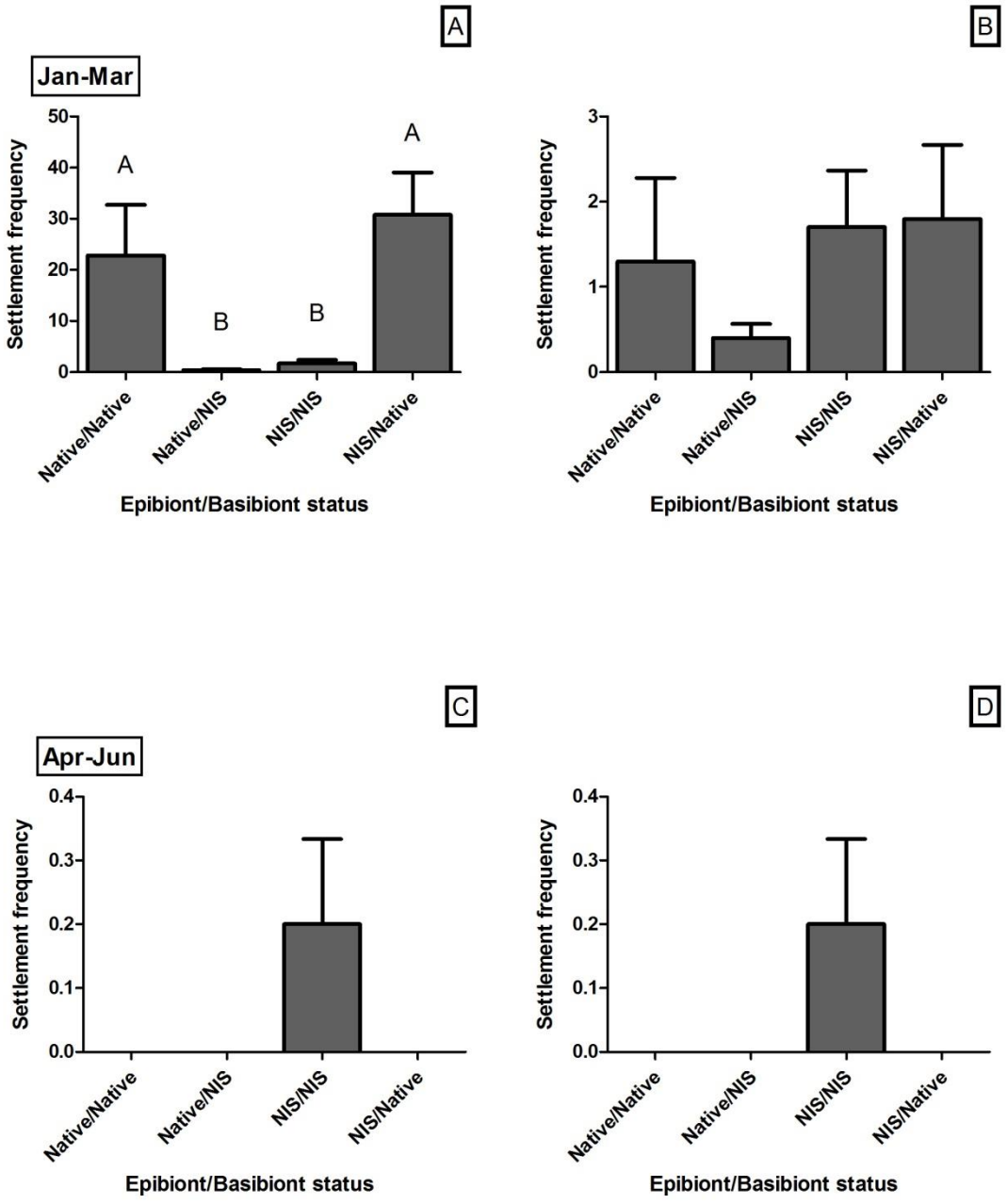

Figure 4.5: Settlement frequency of native/NIS epibiotic settlement on native/NIS basibionts across 3-month treatments during four settlement periods (+SE), when A) Jan-Mar with *Molgula ficus* present; B) Jan-Mar without *Molgula ficus* present; C) Apr-Jun with *Molgula ficus* present; and D) Apr-Jun without Molgula ficus. Note: letters denote significant differences.

4.3.1.2 Seasonal influence 6-month treatments

The 6-month treatment during the Oct-Mar sampling period did not have any native/NIS associations. There was a significant difference between the other epibiont/basibiont associations, with and without *M. ficus* ($H_{[3]}$=23.59, $p < 0.0001$ and $H_{[3]}$= 15.85, $p = 0.0004$ respectively; Figure 4.5A and B). Native/native and NIS/native associations both had significantly greater settlement frequencies than NIS/NIS regardless of whether *M. ficus* was omitted (Dunn's Appendix D, Table 2).

Settlement frequencies between different epibiont/basibiont groups differed significantly for the 6-month treatment with the deployment duration of Jan-Jun ($H_{[4]}$= 34.65, $p < 0.0001$; Figure 4.5C). Native/native and NIS/native associations both had significantly greater frequencies than native/ NIS and NIS/NIS. Analysis of the same treatment with *M. ficus* omitted did not show significant differences ($H_{[4]}$= 7.598, $p = 0.0551$; Figure 4.5D).

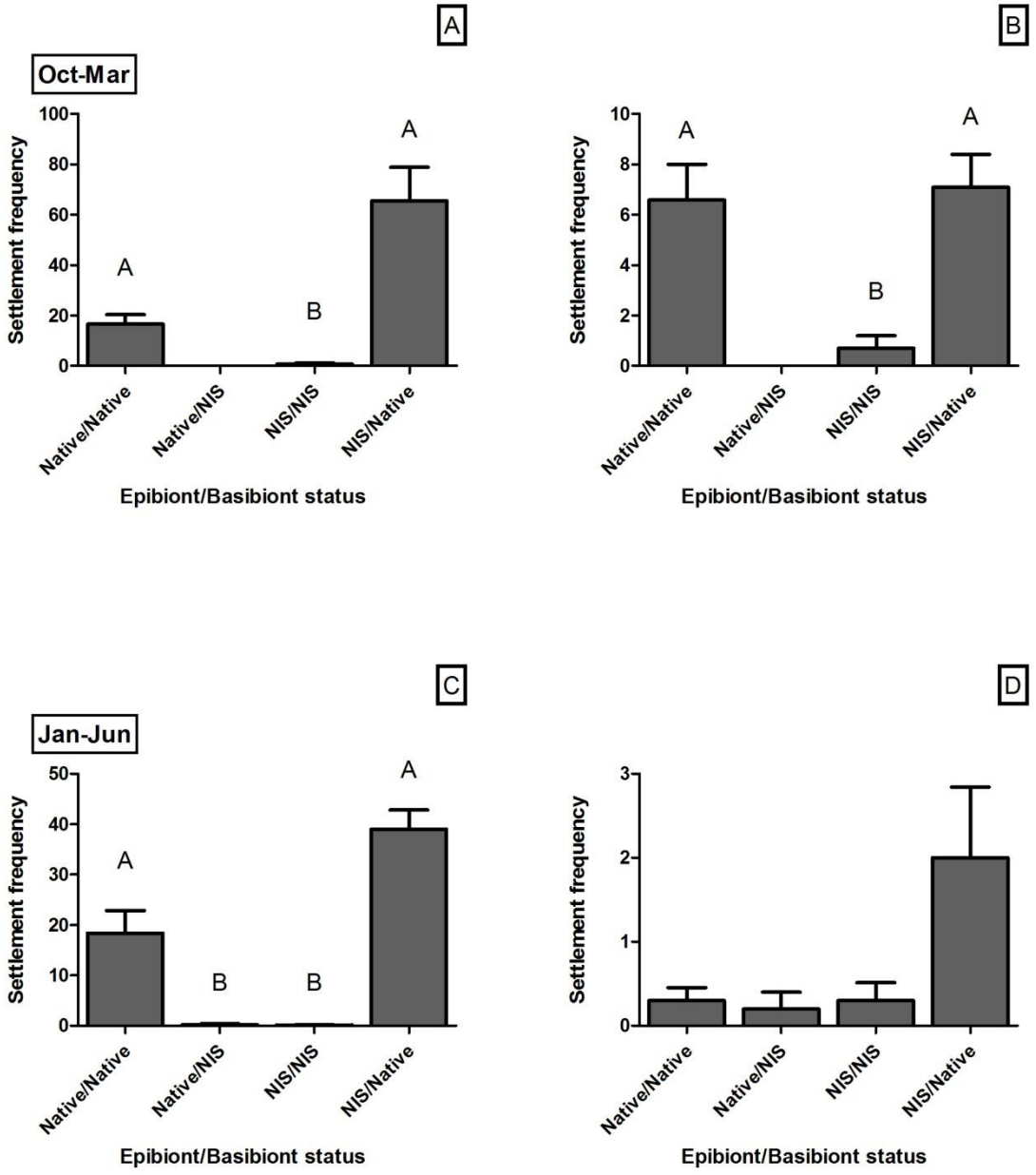

Figure 4.6: Settlement frequency of native/NIS epibiotic settlement on native/NIS basibionts across 6-month treatments during four settlement periods (+SE), for October-March and January-June, when A) Oct-Mar with *Molgula ficus* present; B) Oct-Mar without *Molgula ficus* present; C) Jan-Jun with *Molgula ficus* present; and D) Jan-Jun without Molgula ficus. Note: letters denote significant differences.

No epibiosis was recorded on the native ascidian *M. ficus* for the 6-month treatment during the April-Sep settlement period. However, settlement frequencies between the four epibiont/basibiont associations differed significantly ($H_{[3]} = 11.88$, $p < 0.0078$; Figure 4.6A and B). NIS epibionts on native basibionts were observed to occur significantly more frequently than settlement of native epibionts on NIS basibionts (Dunn's Appendix D, Table 2).

Associations for the 6-month treatment Jul-Dec differed significantly ($H_{[3]} = 28.36$, $p < 0.0001$ Figure 4.6C). Native/native and NIS/native epibiont/basibiont associations both had significantly greater frequencies of epibiosis than native/ NIS and NIS/NIS associations. The same treatment with *M. ficus* omitted was not significantly different (Mann-Whitney U =44.00, p = 0.5036; Figure 4.6D).

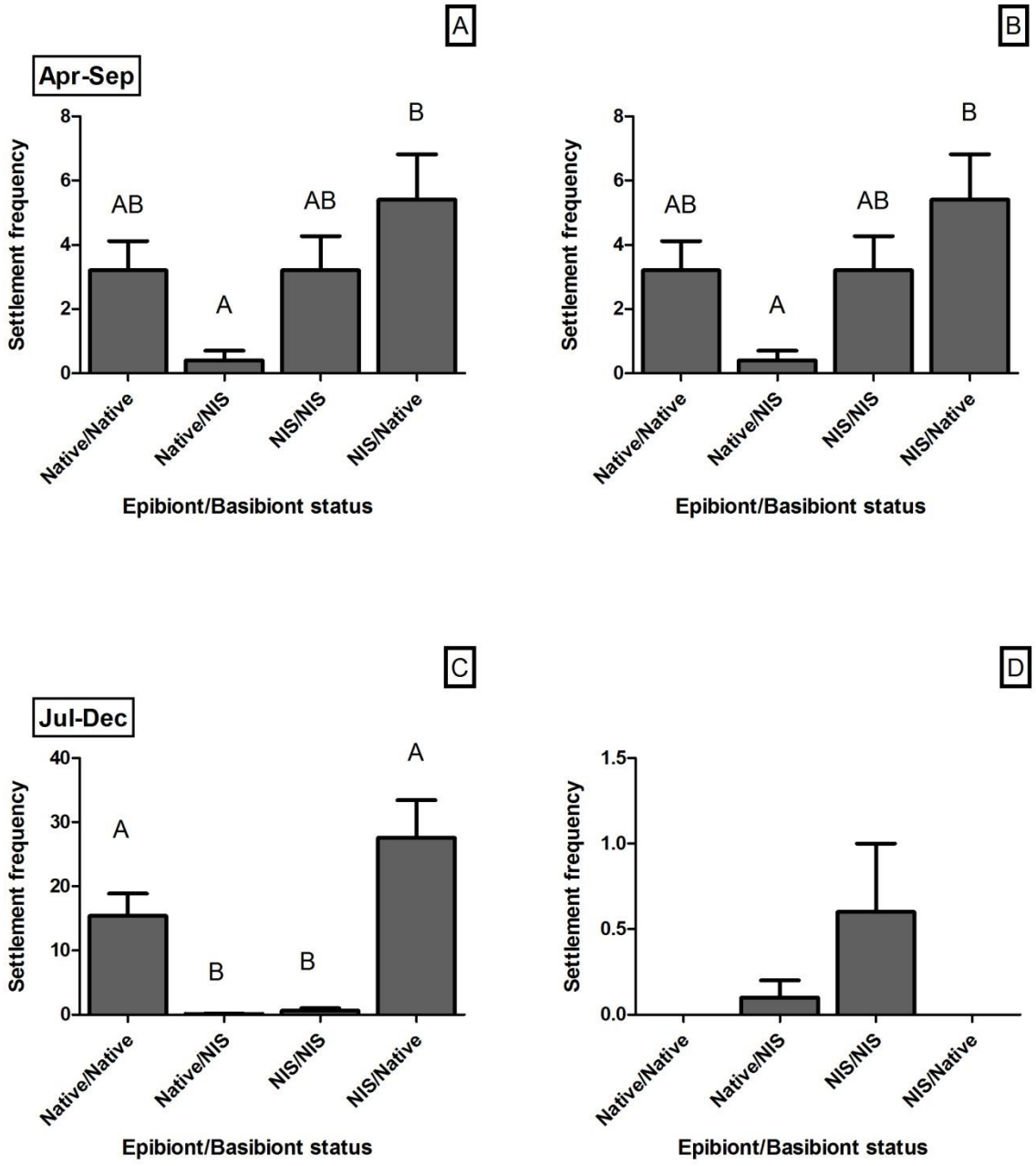

Figure 4.7: Settlement frequency of native/NIS epibiotic settlement on native/NIS basibionts across 6-month treatments during four settlement periods (+SE), when; when A) Apr-Sep with Molgula ficus present; B) Apr-Sep without Molgula ficus present; C) Jul-Dec with Molgula ficus present; and D) Jul-Dec without Molgula ficus. Note: letters denote significant differences.

4.3.2 Epibiont ratio settlement

Settlements across all epibiont species for 3-month treatments differed significantly ($H_{[22]}$=43.24, p=0.0007). Further analysis showed that the NIS bryozoan *Bowerbankia gracilis* and the native ascidian *Herdmania momus* settled onto bare space at greater densities than the two native hydroid species *Eudendrium capillare* and *Obelia* sp 1 (Figure 4.7; Dunn's Appendix D, Table 3).

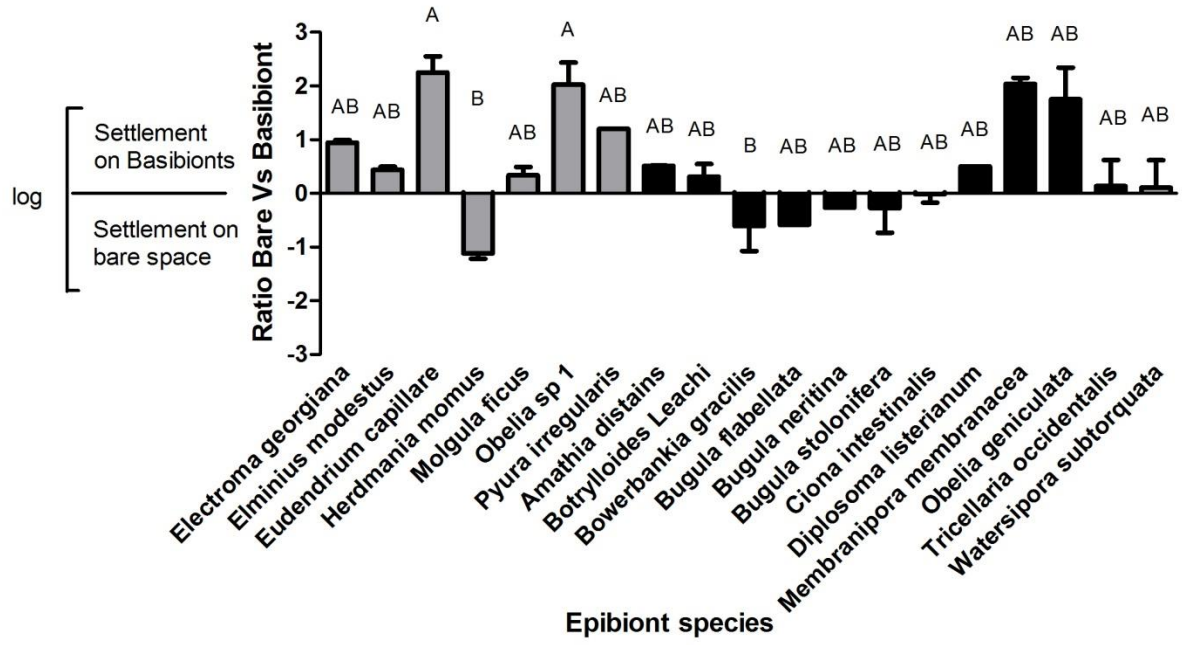

Figure 4.8: Individual species ratios of settlement for all recorded epibionts recorded from 3-month treatments across all basibionts (epibionts settlement onto bare space versus recruitment onto unoccupied space) (+SE). Note: Grey = Native species and Black = NIS.

Ratio settlement of the combined native species onto basibionts compared to bare space during the 3-month treatments was significantly greater than that of the combined NIS

($t_{[85]}$=4.518, p= 0.0001; Figure 4.8). Native species showed a strong preference to settle on basibionts while NIS did not.

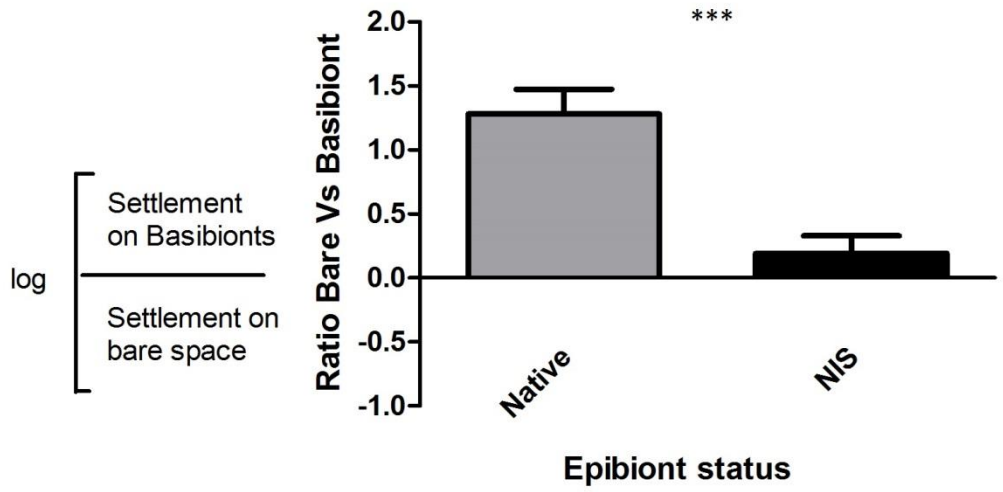

Figure 4.9: Combined ratio settlements of NIS and native epibionts across all basibionts versus recruitment onto bare space for the 3-month treatment (+SE). Note: *** indicates significance between variables.

The ratio settlement of epibionts from the 6-month treatments was significantly different ($H_{[20]}$=36.02, p=0.0153; Figure 4.9; Dunn's Appendix D, Table 4). Further analysis showed that the native ascidian *Herdmania momus* ratio settlement was significantly different than two species, the native species *Eudendrium capillare* and the NIS *Membranipora membranacea*, which settled at a higher rate onto basibionts.

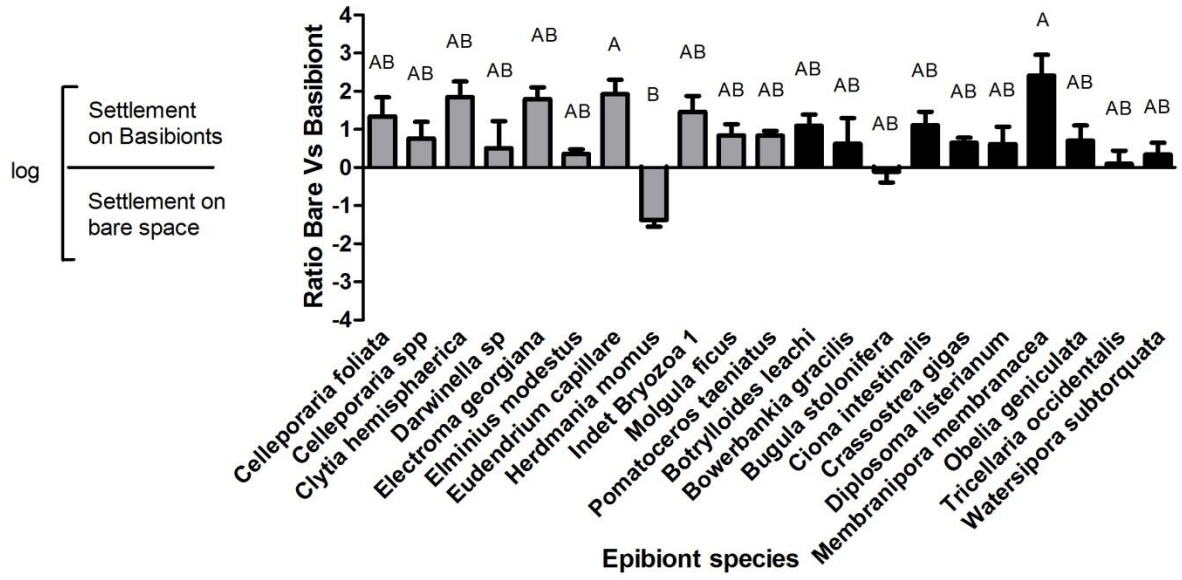

Figure 4.10: Individual epibionts ratios of settlement recorded from 6-month treatments across all basibionts (epibionts settlement onto bare space versus recruitment onto unoccupied space) (+SE). Note: Grey = Native species and Black = NIS.

Both native and NIS of epibionts from the 6-month treatment settled at higher rates on basibionts compared to recruitment of bare space (Figure 4.10). Native species ratio settlement was similar but at a statistically greater rate than that of the NIS ($t_{[112]}$=2.004, p= 0.0475).

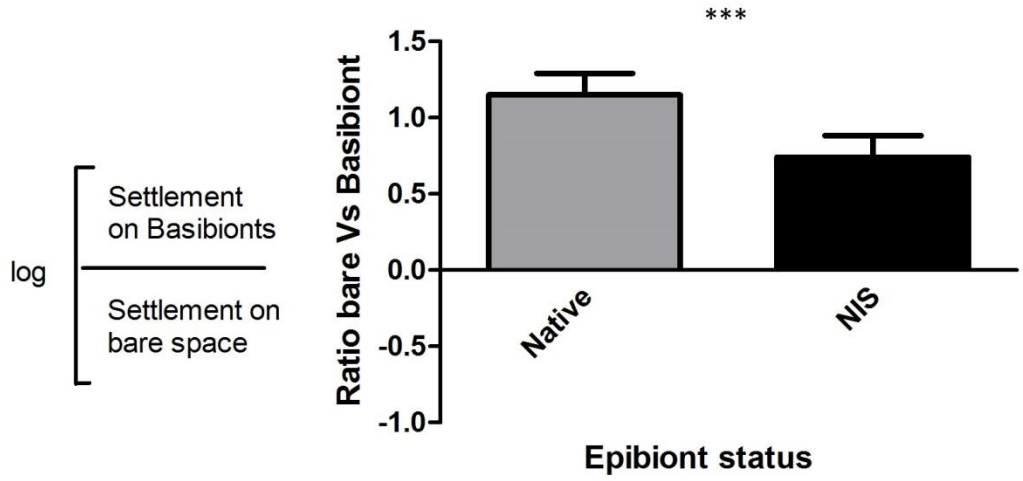

Figure 4.11: Combined species ratio settlement of NIS and native epibionts across all basibionts versus settlement onto primary bare space over the 6-month settlement time (+SE). Note Bar indicates significance.

4.3.3 Combined and grouped epibiont preference

Native species settled approximately two fold more onto basibionts than they did bare space for both 3 and 6-month trials, there was no significant difference between treatments ($t=0.5562_{[76]}$ $p=0.5797$, Figure 4.11A). In contrast NIS recruited on both bare substrate and basibionts at approximately the same ratio for 3-month treatment and settled at approximately two fold more onto basibionts than they did bare space for 6-month treatments. There was a significant difference between treatments $t_{[122]}=2.774$, $p = 0.0064$, Figure 4.11B).

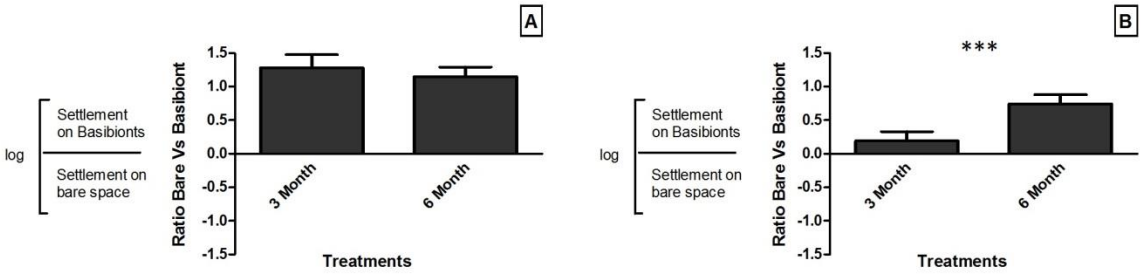

Figure 4.12: Combined ratio settlement of A) native species and B) NIS comparing 3 and 6-month treatments (+SE). Note: *** above columns indicate significant differences between these variables.

Ratios of settlement between different groups (NIS/NIS, NIS/native, native/NIS and native/native) of epibiont/basibiont associations for the 3-month treatment differed significantly ($F_{[3,82]} = 6.222$, $p = 0.0007$; Figure 4.12A; Tukey's Appendix D, Table 5). There was no significant difference in the ratio settlement of NIS on NIS compared to NIS on native ($p = 0.9763$) and native on NIS ($p = 0.4418$) ratio settlement. The ratio settlement of native/native, however, was significantly greater than the ratio settlement of NIS/NIS ($p = 0.0034$) and NIS/native ($p = 0.0024$). There was no significant difference between the ratio settlements of native/NIS compared to native/native ($p = 0.9761$) or Nis/native compared to native/NIS ($p = 0.5435$).

Alternatively, the ratios of settlement of epibionts on basibionts for the 6-month treatment within groups compared to settlement onto bare space did not differ significantly ($F_{[3, 110]} = 1.551$, $p = 0.2054$; Figure 4.12B).

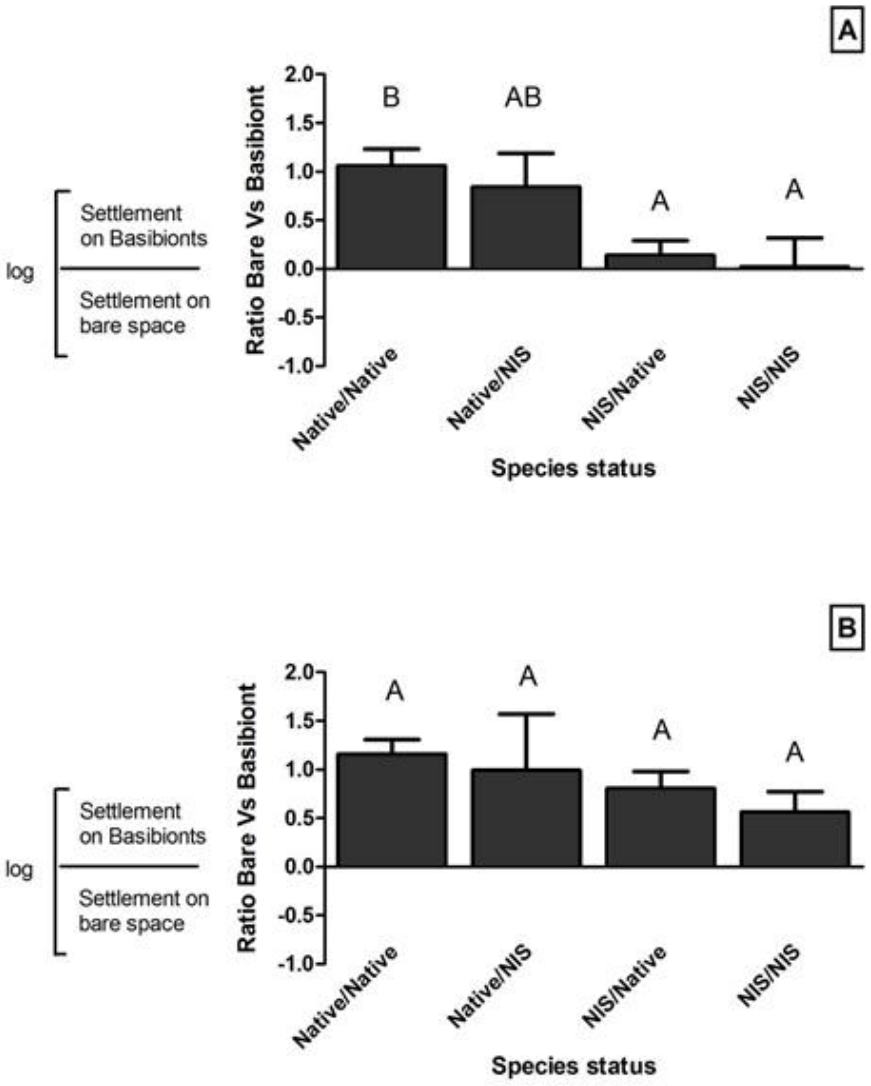

Figure 4.13: Ratio settlement of native and NIS epibiont on native and NIS basibiont compared to primary bare substrate settlement (+SE). A= 3 month treatments, B= 6 month treatments. Note: letters denote variation between groups.

NIS epibionts observed attached to native basibionts compared to recruitment onto bare space was significantly greater with an increased deployment time of 6-months compared to deployment of 3-months ($t_{[34]}$=1.465, p= 0.1522; Figure 4.13A). Ratio

settlement of NIS epibionts observed attached to NIS basibionts however was not significantly different ($t_{[34]}$=1.465, p= 0.1522; Figure 4.13B).

There was no significant difference in the ratio settlement of native species observed attached to native species, ($t_{[75]}$=0.4301, p= 0.6684; Figure 4.13C) or native species observed attached to NIS ($t_{[5]}$=0.2379, p= 0.82140; Figure 4.13D) between treatments.

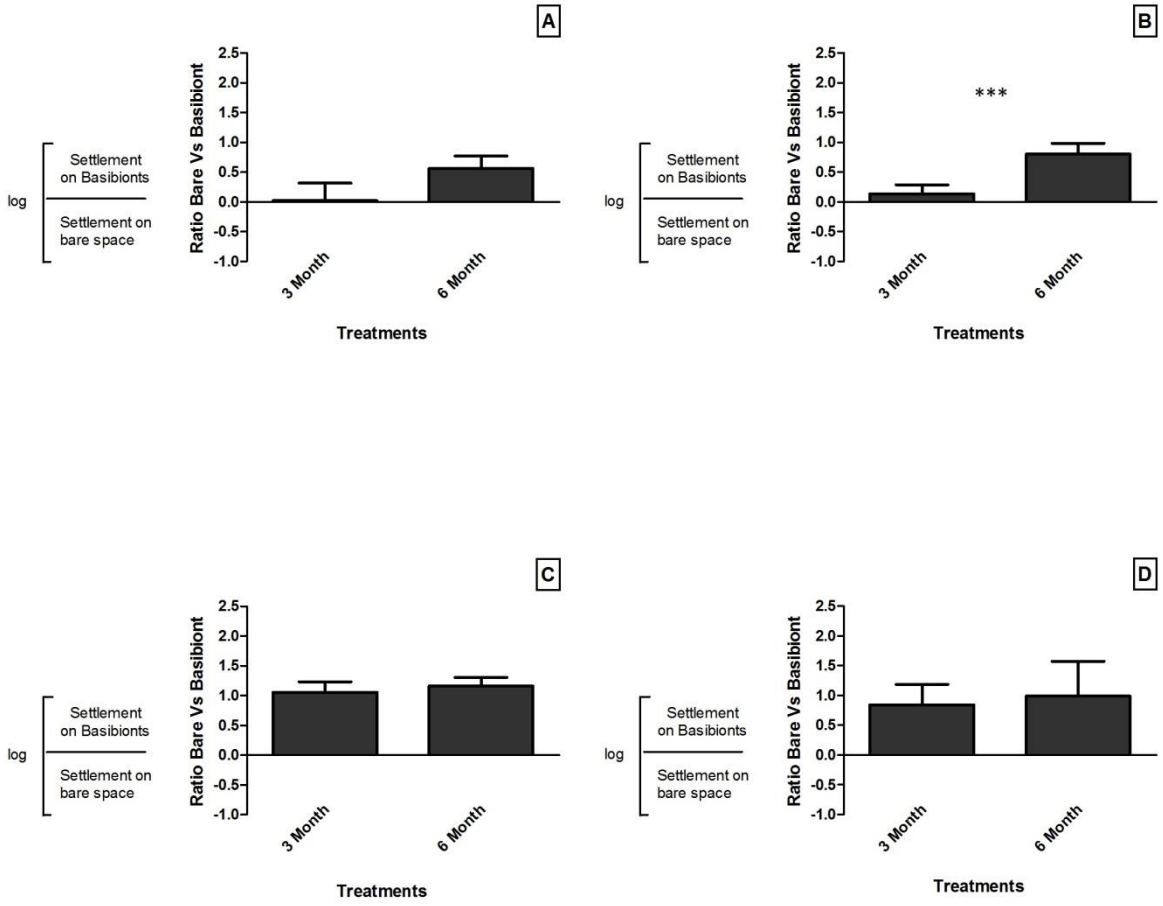

Figure 4.14: Combined settlement of native and NIS epibionts on native or NIS basibiont versus recruitment onto bare space (+SE). Graphs compare three and six month treatments A=NIS epibionts on NIS basibiont B= NIS epibionts on native basibionts, C= Native epibiont on native basibionts and D= Native epibionts on NIS basibionts. Note *** above columns indicate significance difference between these variables.

4.5 Discussion

This chapter aimed to explore differences in epibiotic pressure on native and NIS, whilst simultaneously quantifying the differences in pressure placed by native and NIS epibionts. Moreover this chapter aimed to show difference in settlement preference, with native species hypothesised to show preference to settle on bare space (H7). In contrast NIS are hypothesised to be more opportunistic settlers, only showing preference to settle as epibionts on older substrates where bare space is limited (6-month treatments)(H8).

4.5.1 Epibiotic pressure

I hypothesised that; the frequency of settlement onto native basibionts will be significantly greater than the settlement frequency onto NIS species (H6). Settlement frequency on native or NIS basibionts by all epibionts did differ significantly for both the 3 and 6-month treatments. Settlement onto native species far exceeded settlement onto NIS (Figure 4.1) thus results support the hypothesis. Not all epibiont/basibiont associations have negative impacts on basibiont; for example some epibionts protect basibionts from desiccation (Penhale, 1977), or provide camouflage (Stoecker, 1978). However, in general epibionts tend to result in deleterious effects on benthic sessile species (Wahl and Lafargue, 1990; Harder, 2009). I infer from the results of this study (that examined the available pool of recruits encompassing all potential settlers across available taxa) that, compared to native species, NIS recorded within this study are subjected to less epibiotic pressure. Epibiotic pressure can be inferred to correlate with the potential to experience harm from epibiotic settlement and overgrowth.

4.5.2 Epibiont ratio settlement

I hypothesised at the start of this project that; native epibionts will show preference to settle onto bare space over settlement onto either native or NIS species (H7). Native species that were recorded as living as epibionts were recorded living on basibionts twice as much as those individuals that were living on bare space (Figures 4.8 and 4.10), thus the hypothesis is rejected. There was a statistical association present between native/NIS epibiont settlement frequencies on native/NIS basibionts for the combined 3-month treatments with Molgula included (Figure 4.2A), this association however was not present for the combined 6-month treatment.

Settlement frequency for both the 3 and 6-month treatments were similar in that there seemed to be high levels of settlement on native basibionts by native and NIS epibiont compared to epibiotic pressure on NIS (Figure 4.2). The observed preference of native epibionts to settle on native basibionts but avoid settlement on NIS basibionts suggests that co-evolved recognition exists between native epibionts and native basibionts. Similarly, reduced native epibionts on NIS basibionts may also result from a lack of co-evolved recognition. Much like a parasite/host relationship (Torchin et al., 2003) sessile epibionts have the capacity to regulate a population by reducing the fitness of basibionts (Buss, 1979), thus any reduction in epibiosis may be considered a competitive advantage. Observations made in this chapter in part support the theory that invaders within their invaded region experience a release from natural enemies (Keane and Crawley, 2002; Torchin et al., 2002; Colautti et al., 2004). However future studies need to assess if NIS have fewer epibionts in invaded regions than in their native regions for this theory to be fully investigated.

Observations made with regards to settlement on 3-month plates compared to 6-month settlement plates proved to be an important contribution to this dissertation that has implications for the discipline of marine biological invasions. For example, Chapter 3 illustrates that although recruitment of NIS is higher native species occupied more primary space in 6-month trials (3.20). This result raised the question of, if and how are NIS living within these assemblages? I have hypothesised that; NIS ratio settlement of basibiont compared to bare space will be greater for 6-month treatments compared to 3-month treatments (H8). The ratio settlement (across all 3-month treatments) for NIS was ~1.2 : 1 (basibiont : onto) indicating that NIS show preferences viewing all space (both biogenic and bare) as "free" space. Whereas, settlement for the 6-month treatments was at a ratio of ~1.8 : 1 indicating that on the 6-month treatments NIS show a preference to settle on basibionts, as the ratios were significantly different. This trend was also evident for both a majority of the individual species (Figures 4.7 and 4.9), As such, H8 (NIS ratio settlement of basibiont compared to bare space will be greater for 6-month treatments compared to 3-month treatments) is accepted.

This research used treatments of 3 and 6-months, further treatments (9 and 12-month) were desired however the overall weight of the community on older plates, mainly during retrieval, resulted in the "sloughing" of the samples and therefore this data was not presented in any analysis. It was however observed from these substrates and other substrates within the area (e.g. marina infrastructure) that *Molgula ficus* remained the dominant primary space occupier regardless of substrate age. Additionally it was observed that on the omitted substrates (9 and 12-month) bare space was generally non-existent. It is expected that

epibiosis onto native living substrates would however increase given longer recruitment times.

Within the early stages of a community assemblage (3-months) recruitment onto bare space would be high and the biomass of available "basibionts" is low, while in contrast to this the 6-month treatment assemblages had a greater recruitment/growing time equating to denser populated assemblages (Jackson and Buss, 1975). In this study, space was limited to the settlement plates and it appears that NIS are adapted to fully utilise all available settlement strategies, with epibiosis seeming to be a preferred mode of life given bare space is limited. Success of NIS is often linked to invaders being "opportunistic" and taking advantage of a particular situation, function or trait such as a having a greater tolerances to different abiotic factors such as hypoxia (Schofield and Chapman, 2000), temperature (Zerebecki and Sorte, 2011) or environmental pollutants (Piola and Johnston, 2006b), a reduction in enemies (Keane and Crawley, 2002), or increased competitive advantage (e.g., increased resource consumption; Byers, 2000). This study illustrates that NIS exhibit opportunistic epibiosis and consequently settle on all substrates (i.e., all substrates are available, suitable substrate). The implications of this are important to managers as all substrates can effectively be (bio) fouled by NIS species, not just bare space.

The facilitative role NIS play in the success of other NIS has been widely discussed (Simberloff and Von Holle, 1999; Ricciardi, 2001; Grosholz and Ruiz, 2003; Green et al., 2011), especially with regards to epibiosis (Floerl et al., 2004). In part the results of this chapter support an "Invasion meltdown theory" (e.g., Grosholz and Ruiz 2003), with NIS showing an association to settling on NIS for 3-month treatments (Figure 4.2). This

association was not present within 6-month treatments, however results show that this lack of association results from an increase in settlement of NIS onto native species and not a reduction of NIS settlement onto NIS. It was shown in Chapter 3 that native species occupied significantly more primary space than NIS (Figure 3.20), the lack of NIS on primary space thus may explain the lack of association. Harbours and ports are major points of introductions (Carlton, 1987; Ruiz et al., 1997; Hewitt, 2002; Wotton and Hewitt, 2004), with disturbances often being cited as opening new substrate (Herbold and Moyle, 1986). Understanding of facilitation here may be a key step in understanding invasion succuss.

Differences in substrate preferences between grouped native and NIS, as well as individual species, was determined by examining recruitment onto bare unoccupied substrate versus settlement onto basibionts. The only statistical variation for the 3-month treatments existed between the NIS *B gracilis* and the native *Herdmania momus*, which had different settlement preferences compared to the native's *E capillare* and *Obelia sp*. In general though, native species showed a possible preference to settle on basibionts compared to bare space (Figure 4.7). NIS on the other hand showed less preference to settle on basibionts than native species suggesting that NIS may view settlement substrates differently to native species. The trends observed for individual species was examined further by combining all native and NIS epibionts separately (Figure 4.7), here the difference between native and NIS settlement preference was evident, showing that native species of epibionts show a much stronger preference to settle exclusively as epibionts than NIS.

Environmental conditions of the experimental site are thought to contribute to the degree of success and species diversity within assemblages. The site where settlement plates

for 3 and 6-month treatments were deployed has a strong tidal flow, with areas of high siltation and turbidity. Although hard natural substrates within the sample area contained high levels of hard encrusting species, the settlement of these species onto the experimental plates was lower than I expected. There is considerable evidence that indicates that increased siltation and turbidity can result in an altered species composition, especially for filter feeding invertebrates (Chutter, 1969; Rhoads and Young, 1970).

Molgula ficus (a native ascidian species) was the most prevalent species with the largest overall biomass recorded on the three and six month treatments. Although native to this bioregion, this ascidian is a notable invader in North America (Lambert, 2007; Ruiz et al., 2011) and Chile (Clarke and Castilla, 2000), with impacts to aquaculture recorded due to its intense bio-fouling. *Molgula spp* can thrive in areas where sediment levels are high (leading to siltation and turbidity) (Naranjo et al., 1998). Herein, it is suspected that *Molgula ficus* had a competitive advantage over other invertebrates within the assemblage due to its capacity to thrive in silted environments, and this may help to explain its dominance.

This chapter has demonstrated two functions that epibiosis plays to increase sessile benthic NIS invertebrates success within an invaded habitat. First, the sheer difference in the frequency in which native species are fouled compared to NIS will impact upon a native species ability to feed, reproduce and grow. This in turn may equate to an increased mortality and reduced reproductive capability of natives. In addition to this, the results of this chapter suggest that NIS are opportunistic settlers viewing a greater suite of space as suitable substrate than native species that occupy the same space.

A desired outcome of this chapter was to record epibiotic settlement of native and NIS bryozoan species onto native and NIS bryozoan species. Spatial competition between bryozoans generally involves overgrowth, with mortality the outcome for the losing competitor. As discussed (Chapter 1) consequences of epibiosis onto a bryozoan are similar to that of overgrowth thus settling on top of a competitor not only means suitable substrate but also removes the epibiont from a possible costly competition. Understanding outcomes of such interactions will be beneficial to understand if epibiosis does facilitate the success of some NIS. These interactions however were not observed and as such is the focus of Chapter 5.

CHAPTER 5.
EMPIRICAL EVALUATION OF EPIBIOSIS

5.1 Introduction

Impacts of epibiosis have varying consequences that are generally considered to be species specific (Wahl and Lafargue, 1990; Harder, 2009; Wahl, 2010). As discussed in Chapter 1, one of the most cited theories that aims to explain differences between native and NIS within invaded regions, whilst trying to elucidate reasons behind the success of NIS, is the enemy release hypothesis (ERH) (Maron and Vilà, 2001; Keane and Crawley, 2002; Liu and Stiling, 2006). This regulation of a species by enemies is often coined a regulatory release (Colautti et al., 2004). At the centre of this theory are three assumptions 1) that the impacts from natural enemies are great enough to regulate the density, fitness or competitive ability of a species 2) that impacts on native species outweighs that of the impacts on NIS; and 3) NIS capitalise from this reduction in regulation resulting in a competitive advantage over their native counterparts (Keane and Crawley, 2002).

As a result of less epibiotic pressure an invading species may also experience an indirect release (compensatory release), as resources that were originally spent on defence can be reallocated into other competitive actions (Colautti et al., 2004). Evidence supporting this alternative theory of a trade-off between defensive characteristics to other competitive fitness traits has gained support from several earlier researchers (Bergelson and Purrington, 1996; Strauss and Agrawal, 1999; Colautti et al., 2004).

This dissertation has aimed to show situations where epibiosis is linked to the success of NIS. In doing so it was a desired outcome of research chapters 2 and 4 was to record and observe interactions where native and NIS bryozoans were epibionts on native or NIS basibionts, however these interactions were rare. Chapters 2, 3 and 4 demonstrated that native species generally tend to be subjected to greater pressure from epibionts than NIS.

One of the greatest limiting resources for bryozoans within marine fouling communities is space (Connell, 1961; Dayton, 1971; Jackson, 1977). Overgrowth competition is often associated with this limited resource, with the outcome of overgrowth often being mortality. (Jackson, 1977; Rubin, 1985; Lopez Gappa, 1989). Much like overgrowth, epibiosis results in the growth of one competitor on another creating an overgrowth situation, hence theoretically epibiosis has the potential to result in the mortality of the underlying competitor. As such empirically studying bryozoans to assess difference in epibiotic pressure to determine if native or NIS avoid competition differently (settling on top of a competitor removes an epibiont from a competitive interaction). In this chapter, I hypothesise

H9: Native species will have greater epibiotic pressure than NIS;

H10: NIS will settle on native species, bare space and NIS at similar frequencies;

H11: Native species will show increased preference to settle on native species over settlement onto NIS.

5.2 Methods

Bryozoans were selected as the test species for this experiment because they form a hard substrate that is adequate for growth of other bryozoan species (Jackson, 1977). It is anticipated that there is an evolutionary response exhibited by basibionts in the form of defence, as the growth of an epibiotic bryozoan on the outside structure would most likely lead to the death of the bryozoan basibiont due to inhibiting feeding movements of lophophores (*sensu* Floerl et al., 2004).

5.2.1 Study bryozoans and their field collection

Colonies of reproductively mature bryozoans were collected from the northern and eastern coasts of Tasmania, Australia, between November 2012 and February 2013 (Austral summer). Four sites were sampled (Figure 5.1). Colonies collected comprised of four NIS bryozoan species (encrusting: *Watersipora subtorquata*, *Schizoporella unicornis* and *Cryptosula pallasiana;* and arborescent: *Bugula neritina*) and three native bryozoan species (encrusting: *Celleporaria bispinata* and *Celleporaria foliata* and arborescent: *Bugula dentata*).

Watersipora subtorquata was collected from Swansea public jetty (42° 7'23.41"S - 148° 4'40.27"E) via scuba at a depth of ~2m. Colonies collected were multi-laminar which allowed for species to be removed without damaging the top layer of reproductive and feeding zooids.

Schizoporella unicornis and *B. neritina* were collected from Triabunna deep water jetty (42°31'11.52"S - 147°55'3.40"E) via scuba at a depth of <5m. Colonies of *Schizoporella unicornis* selected were attached to mussel shells. Shells were selected as

colonies lifted off undamaged when the mussel shell was gently flexed (top and bottom twisted in opposite directions). *Bugula neritina* was collected from wooden piles to a depth of <5m, using a sharpened metal paint scraper and taking care not to damage the colony when prying it from the substrate.

Bugula dentata and *Celleporaria bispinata* colonies were collected from Kelso (41° 6'24.79"S; 146°47'55.85"E) via scuba at a depth of ~5-7m. *Celleporaria bispinata* was collected on PVC settlement plates that had been secured to the substrate with aluminium pegs at a depth of 7m a year prior to this collection date (i.e., 2010 - 2011). Again the settlements surface had been sanded using 120 grit sandpaper and plate orientation was horizontal. Settlement side faced down approximately 50mm from the natural substrate. *Bugula dentata* colonies that were attached to small rocks and shells were removed taking care not to harm feeding zooids. These were placed in individual plastic containers to minimise damage to the colonies.

Cryptosula pallasiana was collected from Beauty Point marina (41° 9'26.14"S - 146°49'24.88"E) using settlement plates (which are described in Chapter 3). *Celleporaria foliata* was collected from Inspection Wharf at the Beauty Point marina via scuba at a depth of ~5m. Colonies of *Celleporaria foliata* were multi-laminar which allowed for species to be removed without damaging the top layer of feeding zooids.

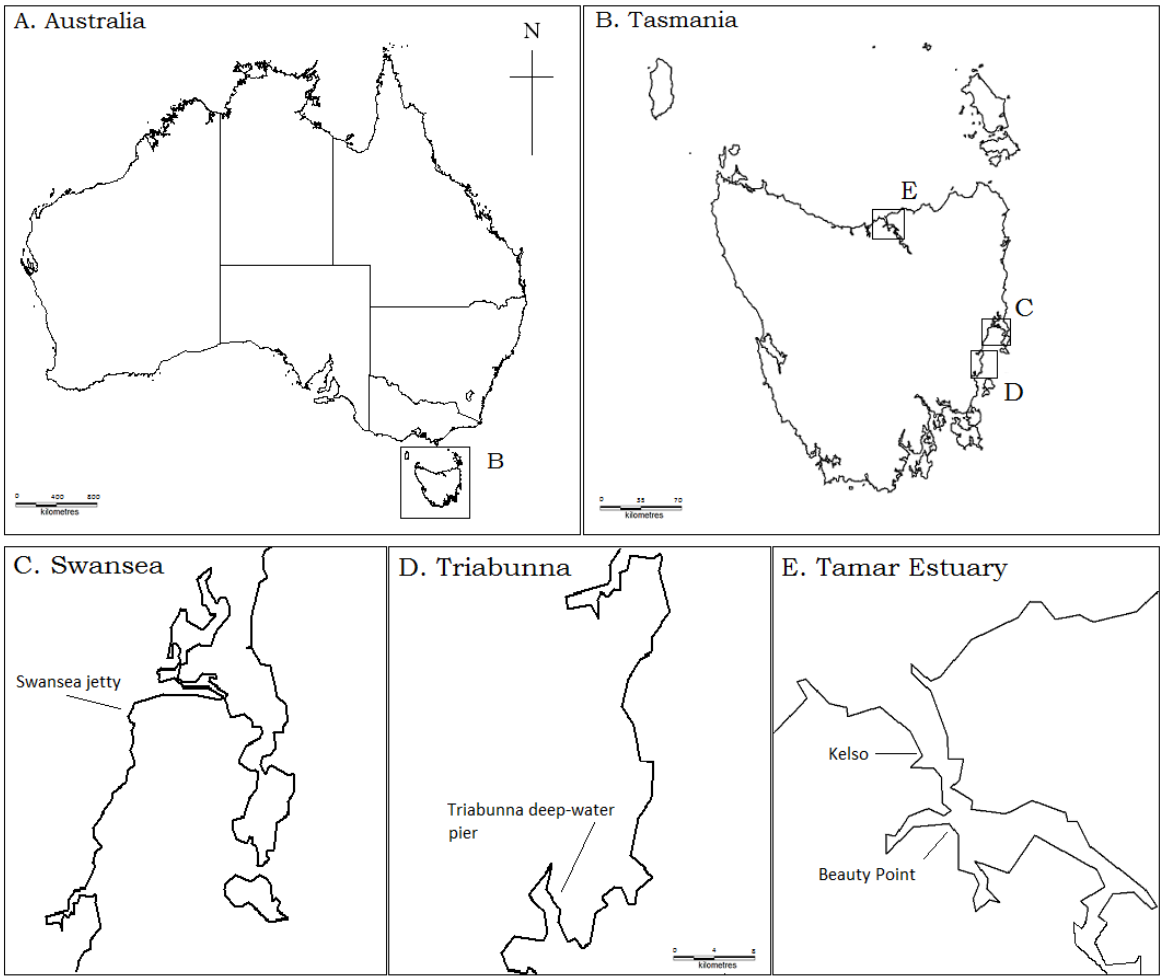

Figure 5.1: Tasmanian sample locations where bryozoan colonies were collected.

Once removed from the water all colonies were placed in separate containers filled with seawater and placed in a cooler to narcotise the specimens and to reduce temperature fluctuations during transport to the University of Tasmania (UTAS) Launceston campus laboratory. Travel time between collection and delivery to the UTAS laboratory for all colonies collected varied between 40min to 2.5h. On arrival at UTAS, colonies were placed into small glass 20L aquariums (W=25 x L=40 x H =20cm) containing an air stone, in a

climate controlled room held at 14°C (equivalent to the ambient early spring water temperature). Bryozoans were left to recover for at least 48h before experimentation began.

5.2.2 Experimental design

5.2.2.1 Experimental substrates (test substrates)

The experimental design used 70 test substrates for each of the five experimental encrusting species, each test substrate contained a living colony; arborescent colonies were not used as substrates. An additional 70 bare slides were conditioned with filtered sea water (FSW) for two weeks as control settlement substrates (10 for each of the seven inoculating species (Cancino, 1986).

In the laboratory, colonies were removed from their collected substrate and segmented into various sizes ranging size of between ~59mm ^{2} to ~496mm^2 with a mean size of 246mm^2. Test substrate (colony) size was determined by analysing images with the software ImageJ (Rasband, 2006). Each segment of a colony included a growing edge of zooids and active feeding zooids. Segments were then gently glued onto a 50 x 76mm plain clear glass slides using a non-toxic Cyanoacrylate glue (Ecotech marine LLC Coral Glue) (Figure 5.2). Care was taken to ensure that only a small amount of glue came in contact with the bottom of the colony and the glue did not come in contact with the colony growing edge.

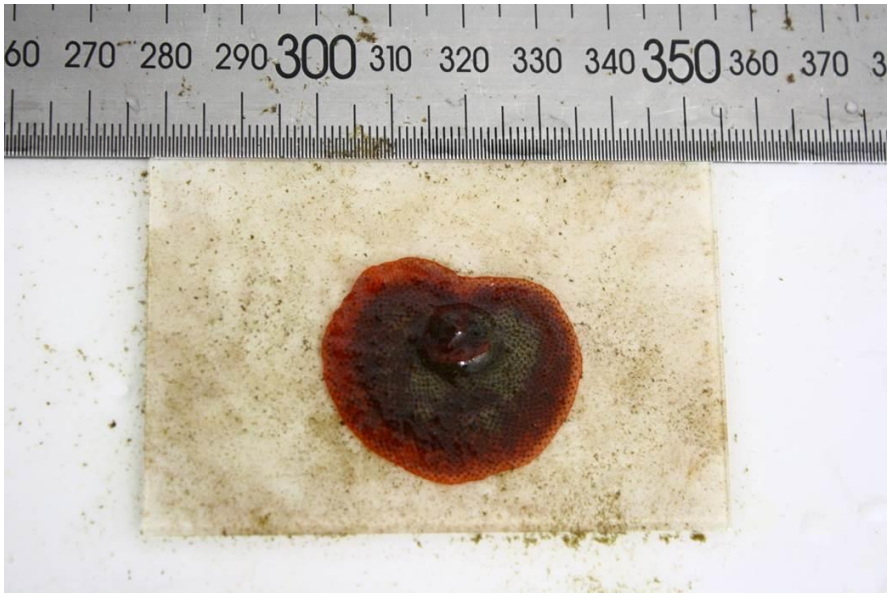

Figure 5.2: Example of experimental test substrate on glass slide (*Watersipora subtorquata)*

Individual slides were placed vertically into modified plastic slide boxes ensuring that faecal matter fell away from the colony (Wood, 1971). Slide boxes held 50 slides; however slides were placed in every second available slot to avoid colonies touching and provide room for growth. Slide boxes had the sides cut down to a height of 10mm to encourage greater water flow. The box bottoms were removed so waste and dead algal cells would not accumulate. Slides were returned to aquaria with FSW and left to recover and grow onto the glass substrate for 2-weeks before being used in settlement assays. Colonies were fed on *Rhodomonas baltica* once daily to a total aquaria concentration of approximately 100 cell μl^{-1}; this medium was changed every second day (Hunter and Hughes, 1993).

5.2.3 Spawning and experimental inoculations

Brooding adult colonies of all of the seven species (five encrusting species and two arborescent species) were required as inoculating species (herein referred to as test larvae).

The release of larvae from brooding adult colonies was induced as a response to light shock (Rittscholt et al 1988). Colonies were placed into aquariums blacked out by black plastic (polyethylene). Aquariums contained 0.2µm filtered seawater and were fitted with an air stone to provide water movement. Bryozoans were placed into the experimental aquaria and left unhindered for 24-48h to adapt to the experimental conditions. After this time, bryozoan colonies were placed in separate beakers with FSW and subjected to a bright ultraviolet (UV) light to induce spawning. Typically, spawning began within 15min to 1h after exposure to light. Initially larvae showed a positive phototactic response and were thus easily collected using a smaller, more directed, light source to attract them and a disposable 2ml pipette. Larvae were collected within 10min of spawning and immediately used to inoculate the experimental test substrates.

For the experiment, each individual slide containing an experimental bryozoan species was placed into a small container with 150ml of FSW with the experimental colony facing down. Containers used tapered in at the bottom which insured the experimental colony was held ≈ 2cm from the bottom of the container. Each container was inoculated with 25 to 30 spawned larvae. After inoculation, the containers were carefully moved back into the climate control room and maintained at a temperature of 14°C +/- 2°C for 24h. Lights remained on within the room, but containers were shaded to best mimic cryptic environments.

Slides were examined after 24 hours, noting the location of the larvae, where locations included: 1) as epibiont; 2) settled within bowl; 3) settled on top of glass; 4) settled

on the bottom of glass; and 5) not settled (deceased). Larvae were considered to be settled if they were attached and had metamorphosed.

5.2.4 Data Analysis

Kruskal-Wallis with Dunns procedures were used to evaluate differences in settlement per (mm^{-2}) between control substrates and treatment substrates where species were present. A Mann-Whitney U test was used when only two independent variables existed. Differences between settlement of native and NIS settling as epibionts or being settled on, as basibionts, compared to control settlement substrates were examined using the ratio of settlement on the test basibiont species mm^{-2} versus the settlement onto control substrates mm^{-2}. This standardised the analyses by allowing any analysis to take into account the size of the basibiont colony. Ratio settlement has been explained in greater depth in Chapter 4.2.2 and figure 4.2.

5.3 Results

5.3.1 Settlement onto test substrates (as epibionts or adjacent to test species) versus controls

5.3.1.1 Encrusting bryozoans

The recorded mean settlement (individuals mm^{-2}) of *C. bispinata, C. foliata, and C. pallasiana* (on test species and adjacent substrate) was significantly different between groups ($H_{[5]}$=12.02, p=0.0345; $H_{[5]}$=31.95, p<0.0001 and $H_{[5]}$=20.649, *p*=0.0009; Figure 5.3 A, B and C respectively. Dunn's Appendix E, Table 1). There was no significant differences between the settlement of *S. unicornis* on control and test settlement substrates ($H_{[5]}$=6.754,

P=0.2396; Figure 5.3D), or between the settlement of *W. subtorquata* on control and test settlement substrates ($H_{[5]}$=7.704, p=0.1733; Figure 5.3E).

Further analysis showed settlement of *C. bispinata* was significantly greater on control substrates than on test substrates where the three NIS test substrates were present. Additionally settlement of *C. foliata* was significant lower on the test substrate with *W. subtorquata* compared to the control substrate and settlement of *C. pallasiana* had increased settlement onto *W. subtorquata* test substrates compared to the control substrate.

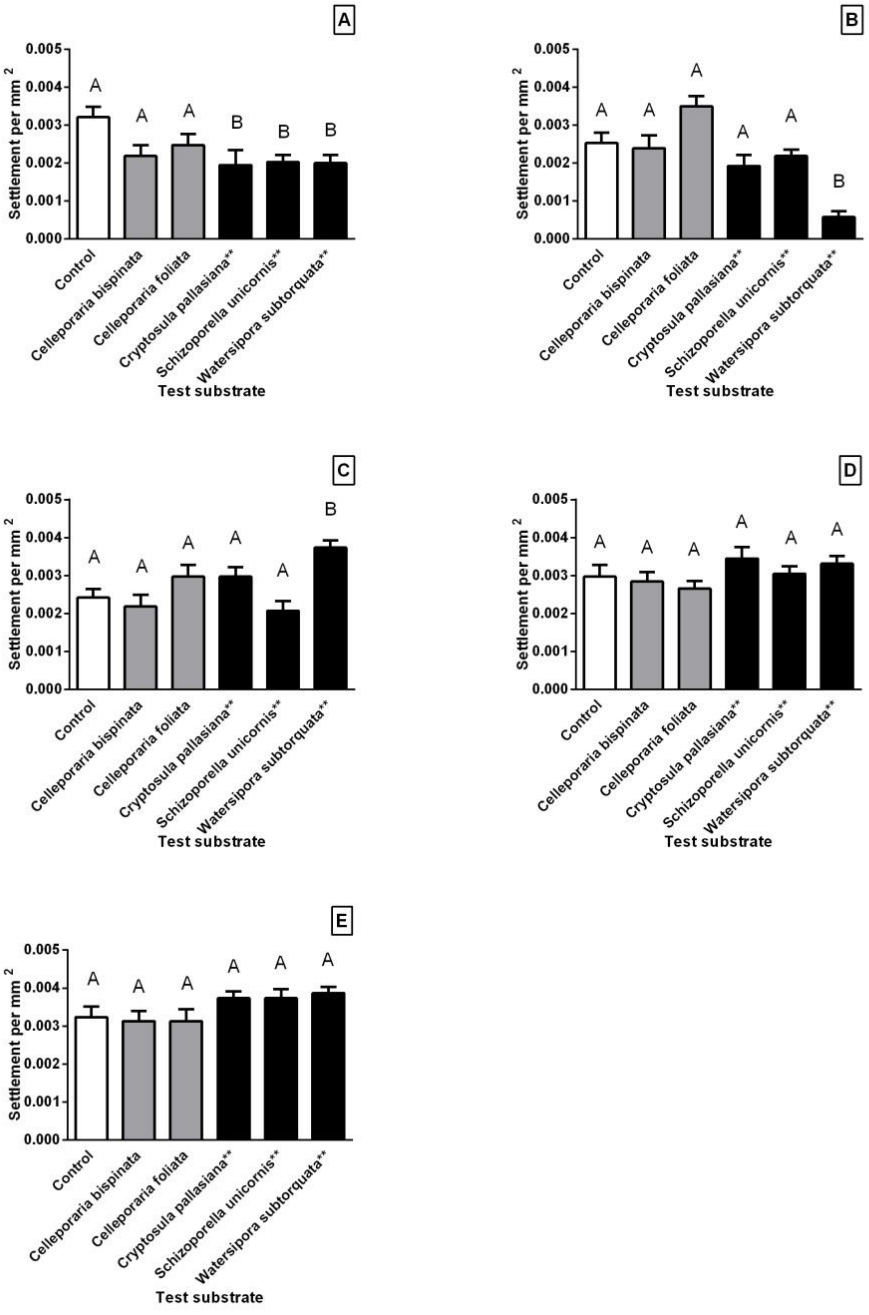

Figure 5.3: Bare space settlement on control versus test substrates (on test species and adjacent substrate) (+SE, N=10), when: A) *C. bispinata*; B) *C. foliata*; C) *C. pallasiana*; D) *S. unicornis*; and E) *W. subtorquata*, . Letters denote variations between control and test substrates.

5.3.1.2 Arborescent bryozoans

Settlement of both arborescent bryozoans *B. dentata* and *B. neritina* was significantly different between groups ($H_{[5]}$=21.68, p=0.0006 and $H_{[5]}$=20.90, p=0.0008; Figure 5.4A and B). Further analysis showed that settlement of *B. dentata* on control substrates was significantly lower than on substrate containing the species *C. bispinata, C. foliata* and *S. unicornis.* Settlement of *B. neritina* on control substrates was significantly lower that settlement on test substrates where *C. bispinata*, *C. foliata* and *W. subtorquata* were present (Dunn's Appendix E, Table 1).

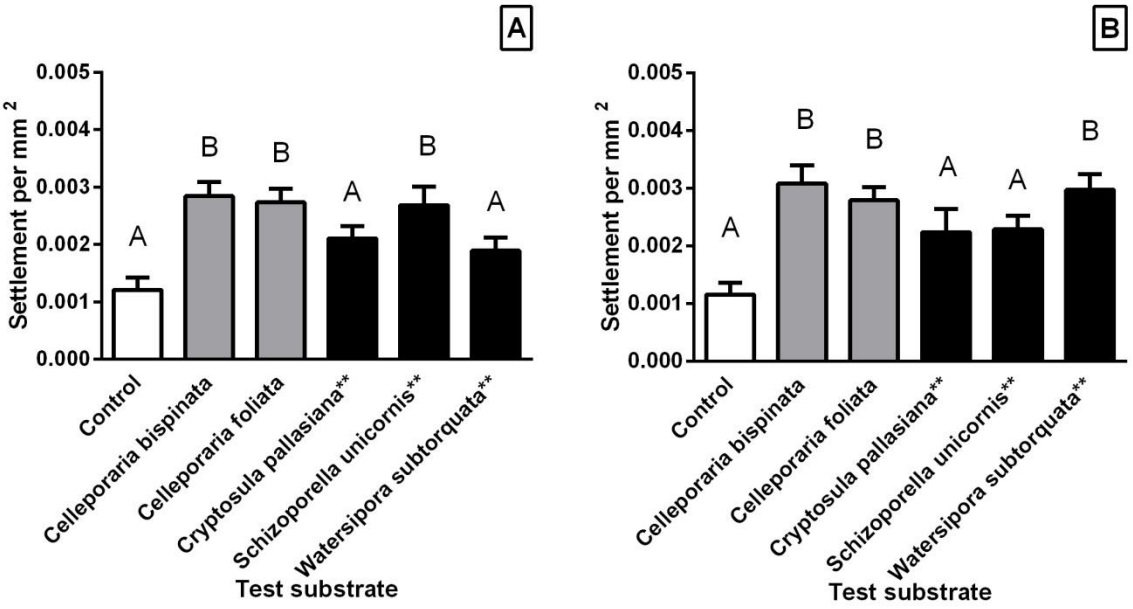

Figure 5.5.4: Bare space settlement on control versus bare space settlement when basibionts were present (+SE, N=10), when: A: *B dentata* and B: *B neritina*. Letters denote variations between control and test substrates.

5.3.2 Epibiont settlement

Native epibionts settled on native basibiont species at greater densities than that of background settlement onto control bare space (Figure 5.5A). In contrast, native epibionts settled on NIS less than settlement onto control substrates. Mean ratios were statistically significantly different (U=1.00, P=0.0008).

NIS species settled on native basibiont species at close to equivalent densities as bare (Figure 5.5B), but settled on other NIS at lower densities than that of control substrates. Ratios settlement here however was not significantly different (U=29.50, P=0.0797).

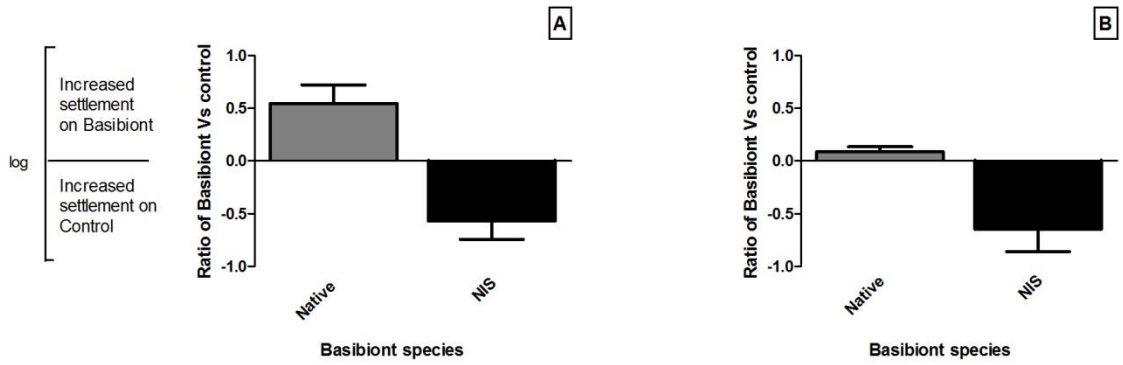

Figure 5.5: Ratio of settlement of for 2 experimental treatments (+SE, N=70), when: A) Native epibionts on native and NIS basibionts versus control settlement substrates; and B) NIS epibionts on native and NIS basibionts versus control settlement substrates.

The combined ratio settlement of native and NIS species on the test settlement substrates (containing native and NIS encrusting species) compared to the settlement on control substrate differed significantly ($H_{[5]}$=40.53, P<0.0001; Figure 5.6), with distinct differences between the epibiotic load on native and NIS basibionts. Native basibiont species

had significantly higher ratios of epibiotic pressure than all of the NIS basibiont species (Dunn's Appendix E, Table 2).

Figure 5.6: Combined native and NIS ratio settlement on different basibionts (+SE, N=70). Note: *** signifies NIS. Letters denote variations between test substrates.

5.3.2.1 Encrusting bryozoans

The larvae of the native species *Celleporaria bispinata* (Figure 5.7A) settlement onto test basibionts versus control substrates (hereon basibiont ratio) differed significantly between different test substrates ($H_{[5]}$=24.12, P < 0.0001; Dunn's Appendix E, Table 3). There was a significant increase in the basibiont ratio settlement of *C. bispinata* as an epibiont on the two native basibionts compared to the two NIS basibionts; there was no settlement onto *W. subtorquata*. Additionally the settlement of *C. bispinata* onto unoccupied

space adjacent to different test bryozoan versus control settlement (hereon adjacent ratio) was not significantly different ($H_{[5]}$=.8715, P<0.9286; Figure 5.7A).

Settlement of *C. foliata* (Figure 5.7B) mimicked that of *C.bispinata,* being significantly different for basibiont ratios between test substrates ($H_{[5]}$=32.38, P<0.0001), and having a significant increase in the ratio settlement as an epibiont on the two native basibionts compared to the NIS basibionts. Similarly *C. foliata* also showed no significant difference in the adjacent ratio between test substrates ($H_{[5]}$=.4510, P=0.3413; Figure 5.7B).

Mean settlement of epibiont ratios for *C. pallasiana* (Figure 5.7C) was not significant difference between groups ($H_{[5]}$=6.506, P=0.1644), however was for adjacent ratios ($H_{[5]}$=20.221, P=0.0005; Figure 5.7C), with the ratio settlement of *C. pallasiana* being significantly greater onto *W. subtorquata* compared to *S. unicornis* and *C. bispinata W. subtorquata*.

There was no significant difference in the epibiont ratio or adjacent ratio between test substrates for S. unicornis ($H_{[5]}$=6.541, P=0.1622, $H_{[5]}$=7.840, P=0.0976 respectively; Figure 5.7D, E) or W. subtorquata $H_{[5]}$=7.840, P=0.0976, $H_{[5]}$=8.828, P=0.0655 respectively; Figure 5.7D, E)

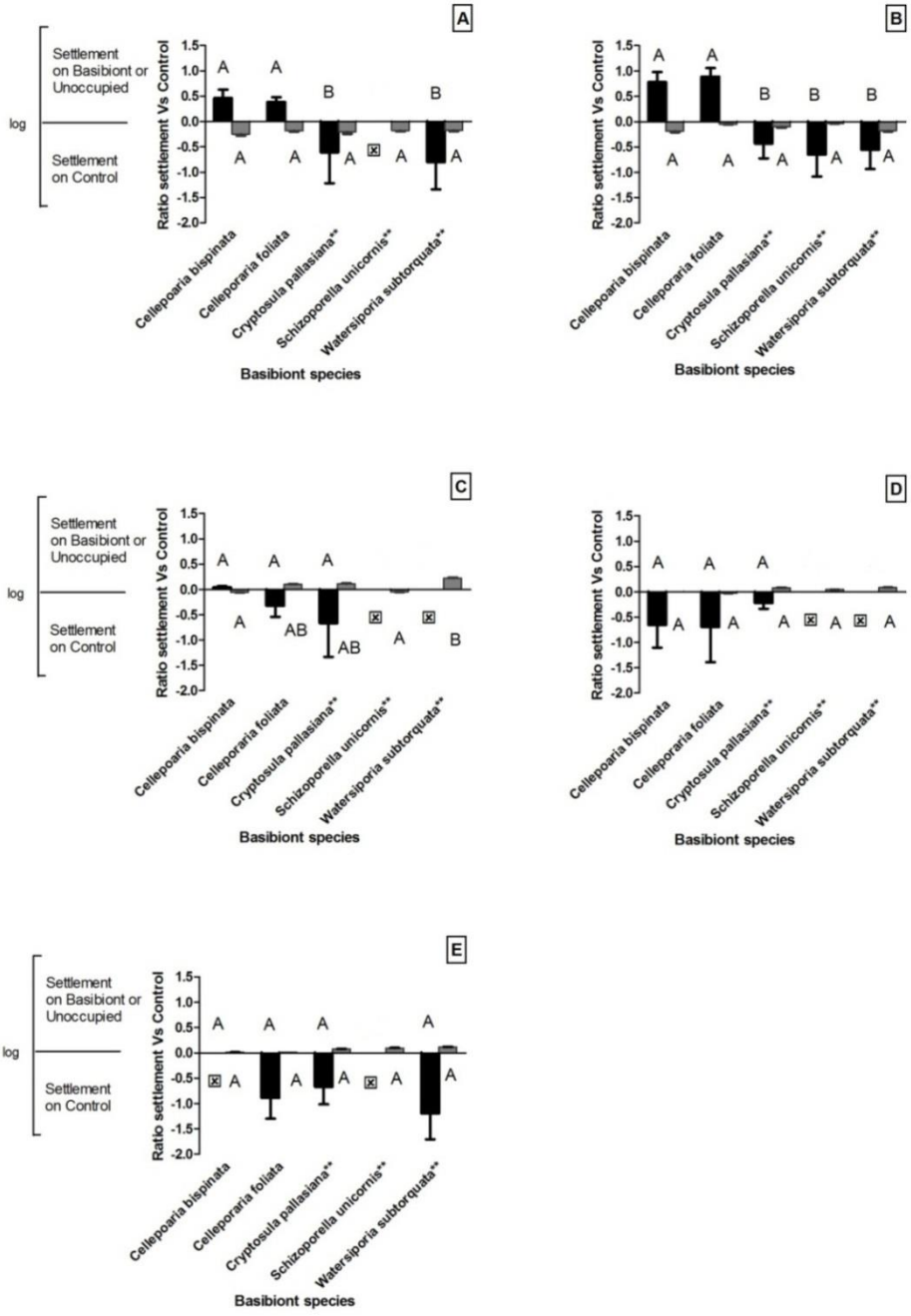

Figure 5.7: Ratio settlement of bryozoan epibionts on bryozoan basibionts versus control substrate settlement (black columns) and ratio settlement of bryozoan on space adjacent to basibionts versus control (grey columns) for encrusting species (+SE, N=10), when: A) *C. bispinata*; B) *C. foliata*; C) *C. pallasiana*; D) *S. unicornis*; and E) *W. subtorquata*. Letters denote variations between groups (top for black columns, bottom grey columns)* signifies NIS. x on graph indicates no ratio settlement.

5.3.2.2 Arborescent bryozoans

Bugula dentata (Figure 5.8A) showed preference to settle on bare space as opposed to any of the basibionts and did not settle on *S. unicornis* at all. There was however no statistically significant difference in the basibiont ratio or adjacent ratio ($H_{[3]}$=1.507, p=0.6806 and $H_{[4]}$=8.008, p=0.0913; Figure 5.8A)(Dunn's Appendix E, Table 4). Likewise there was no significant difference in either ratios for *B. neritina* ($H_{[3]}$=8.008, p=0.0913 and $H_{[4]}$=5.327, p=0.2554; Figure 5.8B).

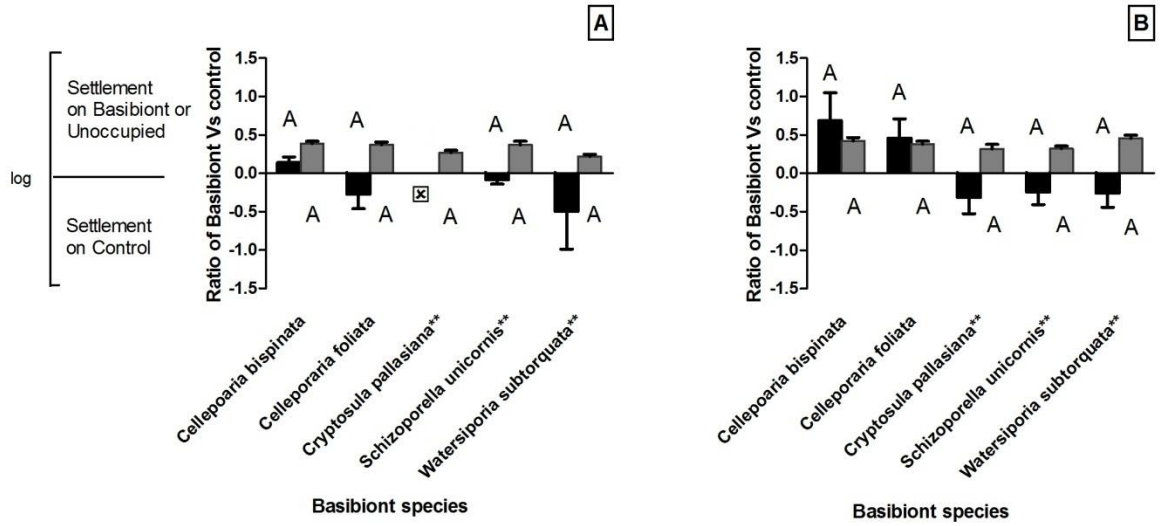

Figure 5.8: Ratio settlement of bryozoan epibionts on bryozoan basibionts versus control substrate settlement (black columns) and ratio settlement of bryozoan on space adjacent to basibionts versus control (grey columns) for arborescent species (+SE, N=10), when: A) B. dentata; and B) B. neritina. Letters denote variations between groups (top for black columns, bottom grey columns)* signifies NIS. X on graph indicates no ratio settlement.

5.3.3 Basibiont analysis

Settlement of different test larvae onto *C. bispinata* versus control substrate settlement (hereon epibiont ratio) or settlement onto adjacent versus control substrates (hereon adjacent

ratio) both differed significantly ($H_{[6]}$=17.25, P=0.0036 and $H_{[6]}$=50.13, P<0.0001, respectively ; Figure 5.9A and B). Specifically, *C. bispinata* showed greater preference to settle on *C. bispinata* than *S. unicornis or W. subtorquata.* Additionally the arboresent bryozoans settled on control substrates less than settlement adjacent to *C. bispinata* compared to *C. bispinata* and *C. foliata.* Moreover the two arborecent species preference to settle on substrates adjacent to *C. bispinata* was greater than all species except *C. pallasiana* (Dunn's Appendix E, Table 5).

Mean epibiont ratio settlement of all larval on the three encrusting NIS test basibionts *C. pallasiana*, (Figure 5.9C), *S. unicornis* (Figure 5.9D) and *W. subtorquata* (Figure 5.9E) followed similar trends, with all inoculated larvae species settling on the control substrate at greater densities than any of the test species. There was no statistically significant difference between epibiont ratios between groups for *C. pallasiana, S. unicornis and W. subtorquata* ($H_{[6]}$=4.414, P=0.6209; $H_{[6]}$=8.627, P=0.1957 and $H_{[6]}$=4.810, P=0.5685; Figure 5.9 C, D and E). However, there was significant differences in the adjacent ratio settlement for the same three species ($H_{[6]}$=32.21, P<0.0001; $H_{[6]}$=49.88, P<0.0001 and $H_{[6]}$=53.14, P<0.0001, respectively; Figure 5.9 C, D and E). Further analysis showed that the two native inoculates settled on control substrates at higher densities than the two arboresent species when the test substrate *C. pallasiana* was present, and at higher densities than all other test larvae when *S. unicornis* was present. Moreover the two arboresent species both had increased settlement onto adjacent space than other test larvae when W. *subtorquata* was present.

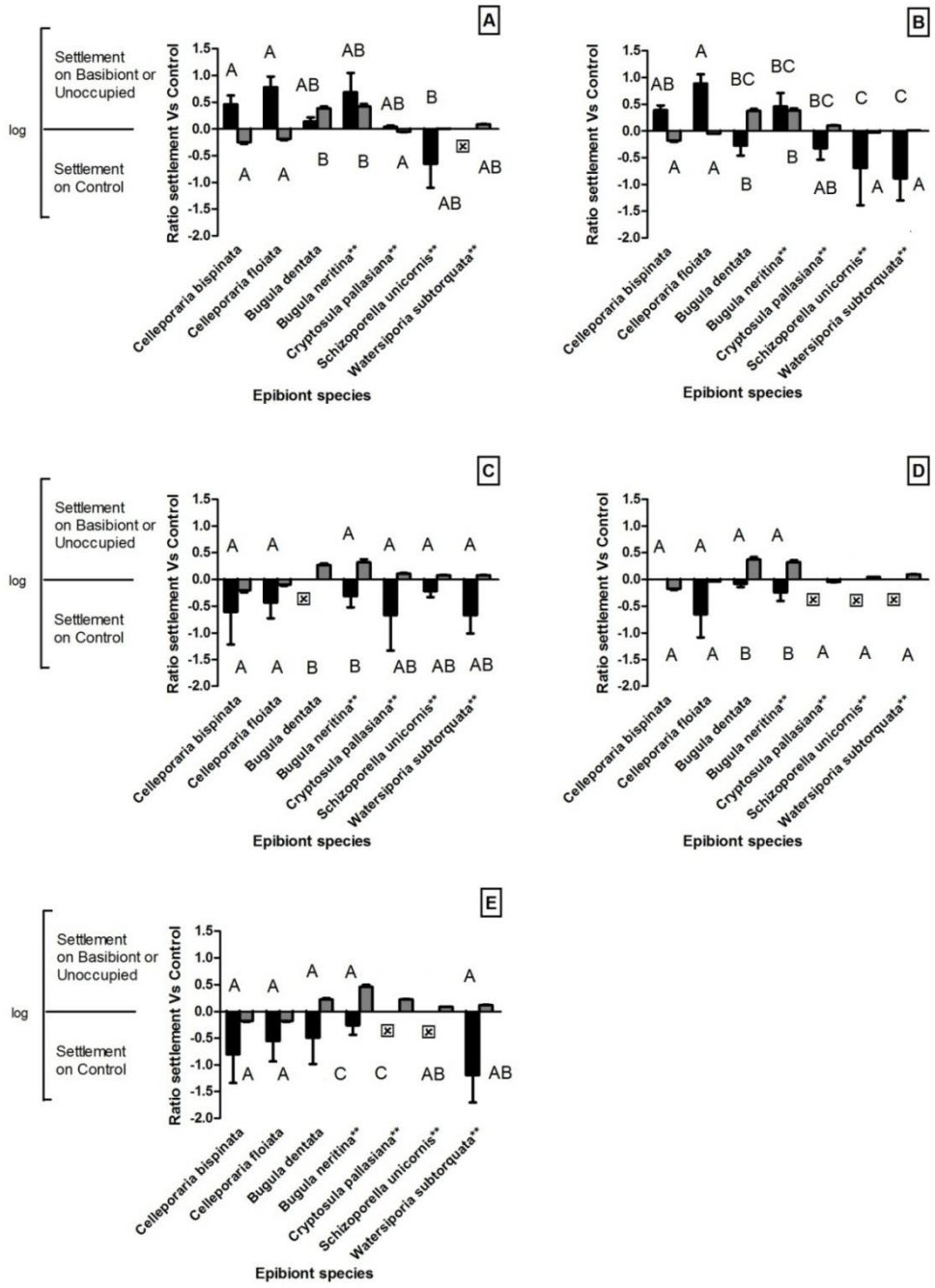

Figure 5.9 : Ratio settlement of individual bryozoan epibionts on bryozoan basibionts versus control substrate settlement (black columns) and ratio settlement of bryozoan on space adjacent to basibionts versus control (grey columns) for encrusting species, (+SE, N=10), when: A) *C. foliata*; B) *C. bispinata*; C) *C. pallasiana*; D) *S. unicornis*; E) *W. subtorquata*. Letters denote variations between groups and black denotes basibiont versus control; grey denotes unoccupied versus control. * signifies NIS and x on graph indicates no ratio settlement.

5.3.4 Larval mortality

The percentage of larval mortality of native species in settlement tests conducted with bare control substrate was significantly greater than the larval mortality of NIS under the same conditions (Mann Whitney U=368.5, *P*=0.0060; Figure 5.10A). Similar tests conducted on test substrates where basibiont species were present resulted on greater amounts of larval mortality compared to control substrate; however, these tests followed the same trend, with native larval mortality being significantly greater than NIS larval mortality (U=7535, *P*<0.0001; Figure 5.10B).

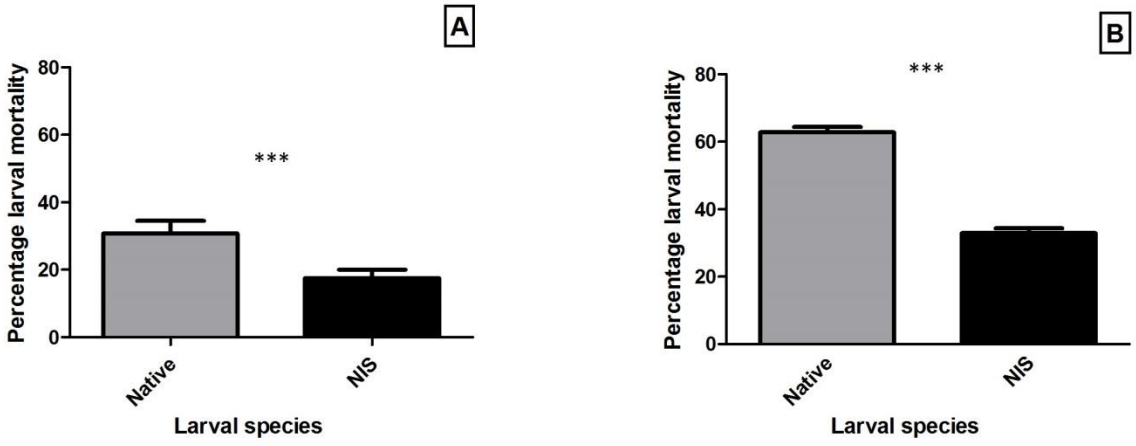

Figure 5.10. Larval mortality of (+SE): A) native and NIS on control substrate; and B) native and NIS on substrate where test species were present. Note *** above columns indicate significant differences between these variables.

There was no significant difference in the proportion (%) of larval mortality of the combined native species when the test substrate contained either a native or NIS test species

(U=2417, *P*=0.2784; Figure 5.11A), or of NIS larvae when either a native of NIS test species was present (U=4661, *P*=0.6927; Figure 5.11B).

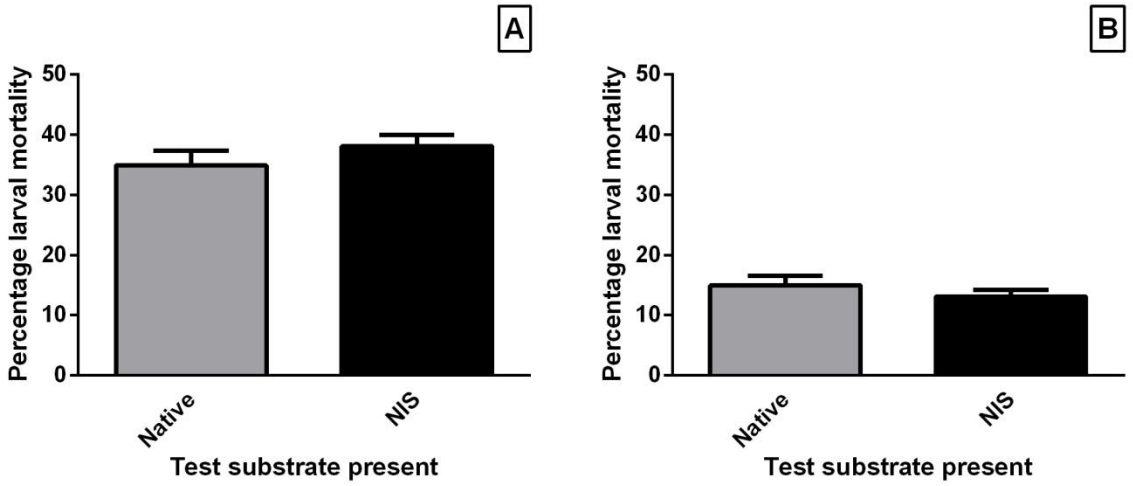

Figure 5.11. Larval mortality of: A) native larvae where native or NIS test substrates were present; and B) NIS larvae where native and NIS test substrates were present.

There was a significant difference in the percentage of larval mortality between different bryozoan species when inoculated onto bare control substrate ($H_{[5]}$=54.94, P<0.0001; Figure 5.12. Dunn's Appendix E, Table 6). Larval mortality of *W. subtorquata* and *S. unicornis* were both significantly lower than all other species apart from *B. dentata* and each other. Additionally, *B. dentata* had significantly lower larval mortality than *C. bispinata.*

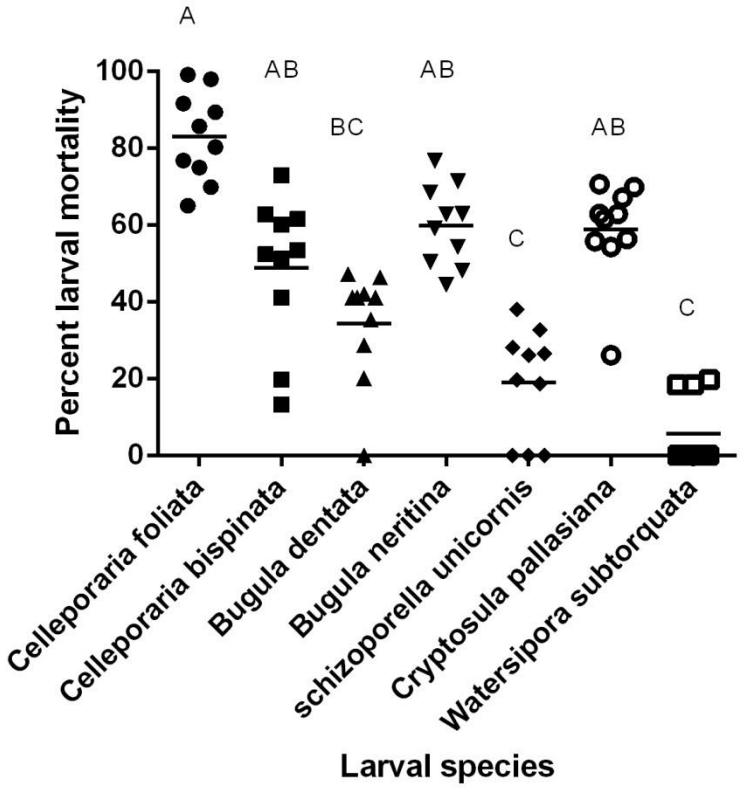

Figure 5.12. Larval mortality of bryozoan larvae species when inoculated onto a bare control substrate (+SE, N=10). Different data points represent mortality for each replicate.

5.3.4.1 Encrusting bryozoans

Larval mortality of *C. bispinata* between different test substrates and control substrates differed significantly ($H_{[5]}$=16.76, P=0.0050; Figure 5.13A), with *C. bispinata* having significantly higher larval mortality when *C. pallasiana* was present compared to the control substrate. Larval mortality of *C. foliata* between test substrates and control settlement substrates was also significantly different ($H_{[5]}$=19.32, P=0.0017; Figure 5.13B). Mortality of *C. foliata* was lower on substrates where *S. unicornis* compared to the control substrate.

Larval mortality of *C. pallasiana* between test substrates and control settlement substrates was significantly different ($H_{[5]}$=18.41, P=0.0025; Figure 5.13C. Dunn's Appendix E, Table 7), with *C. pallasiana* having significantly lower larval mortality when *S. unicornis* and *W. subtorquata* were present compared to the control substrate. There was no significant difference in larval mortality between control settlement substrates and settlement substrates where a test species was present for *S. unicornis* and *W. subtorquata* ($H_{[5]}$=5.980, P=0.382 and $H_{[5]}$=2.441, P=0.7854; respectively Figure 5.13D and E).

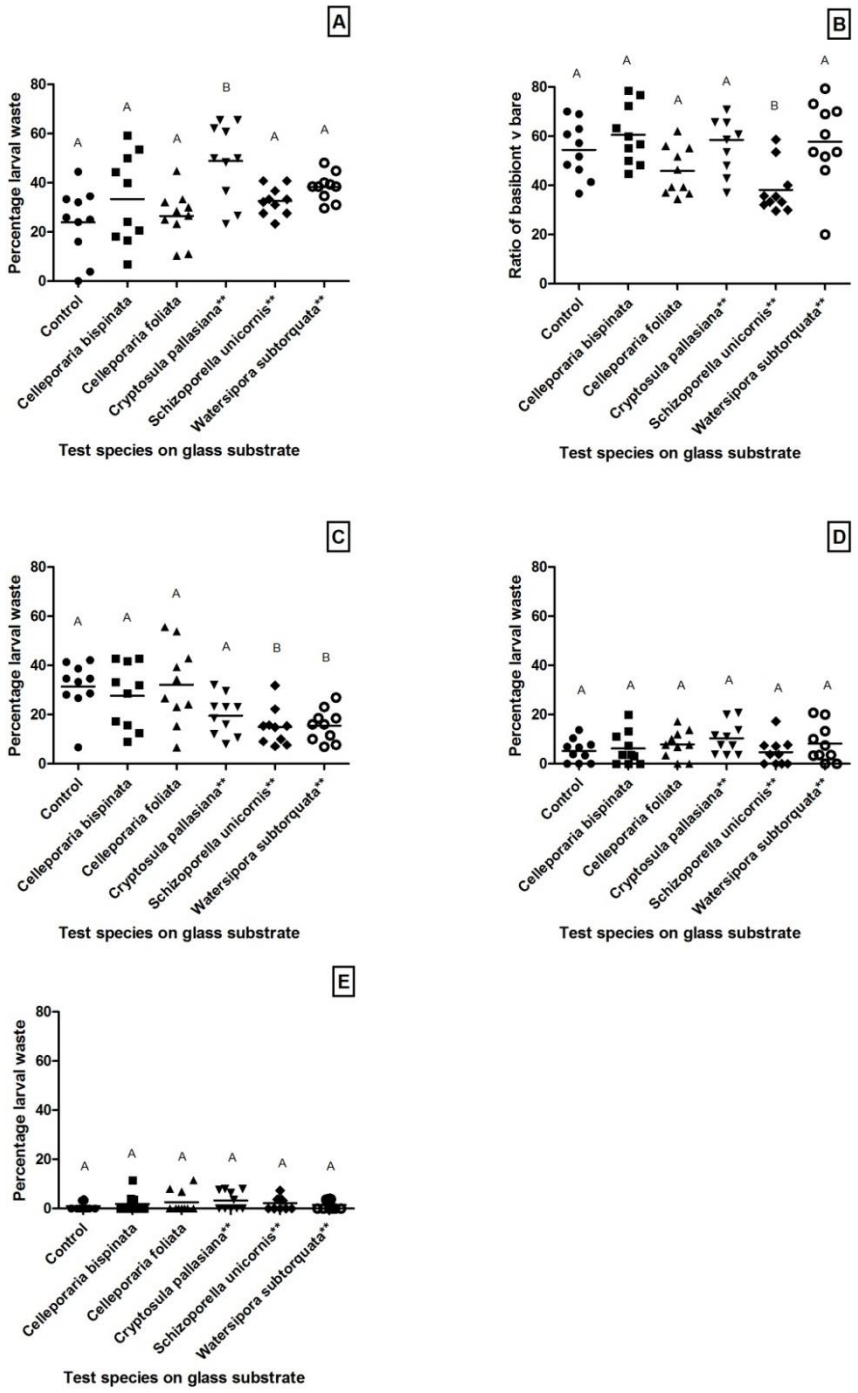

Figure 5.13. Larval mortality (%) of bryozoan species A) *C. foliata*; B) *C. bispinata*; C) *B. dentata*; D) *B. neritina*; E) *C. pallasiana*; F) *S. unicornis*; and G) *W. subtorquata* when living test substrates are present compared against control substrates (+SE, N=10). Different data points represent mortality for each replicate. Note: * signifies NIS.

5.3.4.2 Arborescent bryozoans

There was no significant difference in larval mortality between control settlement substrates and settlement substrates where a test species was present for *B. dentata* and *B. neritina* ($H_{[5]}$=8.682, P=0.1224 and $H_{[5]}$=10.43, P=0.0639. respectively; Figure 5.14A and B).

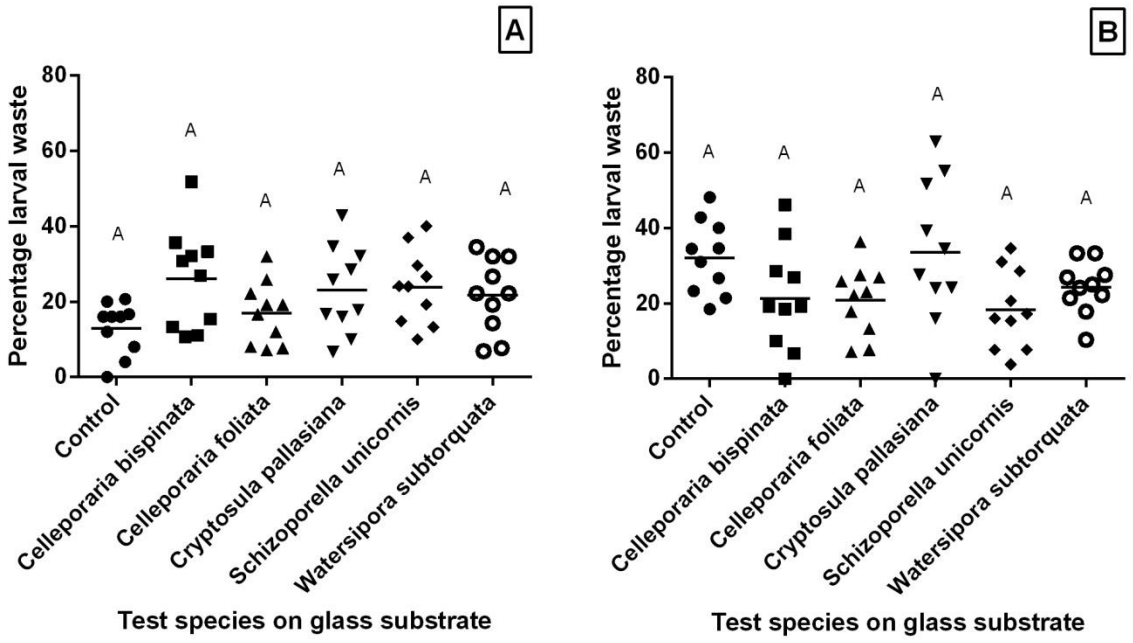

Figure 5.14: Larval mortality (%) of bryozoan species A) *B. dentata*; and B) *B. neritina* when living test substrates are present compared against control substrates (+SE, N=10). Different data points represent mortality for each replicate. Note: * signifies NIS.

5.4 Discussion

It was shown in chapter 4 that NIS tend to be opportunistic settlers in that they view a larger suite of space as suitable substrate than native. In this chapter, it is hypothesised; NIS will settle on native species, bare space and NIS at similar frequencies (H10) inferring that NIS have a competitive advantage as they view all substrate as being "free"/available space. In

contrast, it is hypothesised; native species will show increased preference to settle on native species over settlement onto NIS (H11).

This chapter's research has illustrated numerous advantages that NIS sessile encrusting species have over ecologically similar native species. The manipulative experiments design has allowed for the determination of native and NIS larval responses to the presence of potential competitors. Moreover this experiment illustrates differences in competitive pressure that native and NIS encrusting sessile species endure from epibionts. Initial control experiments illustrated differences in the settlement of native and NIS bryozoan larvae between a control substrate and substrates where test species were present.

The presence of *W. subtorquata* impacted the settlement of two of the test species: the native *C. foliata* and NIS *C. pallasiana,* compared to the control settlement substrates with contrasting effects. For the native species *C. foliata,* settlement was depressed by the presence of *W. subtorquata* yet *C. pallasiana* settlement was significantly increased (Figure 5.3B and C). The reduction in the overall settlement of the native bryozoan larvae *C. foliata* when in the presence of *W. subtorquata* is in contrasts to observations several observations within literature that suggest that *W. subtorquata's* three-dimensional growth provides suitable hard substrate for both natives and NIS (see Floerl et al., 2004; Stachowicz and Byrnes, 2006).

In the present study, *C. foliata* appeared to actively avoid settlement on or adjacent to *W. subtorquata* when compared to the control substrate, which may be viewed as a response that is profitable to *W. subtorquata.* First, *W. subtorquata* avoids possible mortality from overgrowth from *C. foliata*; and second, this may result in less contact interactions and a

greater area available to grow, increasing biomass and reproductive capability. Adequate space to settle is a common limiting resource for many bryozoan species (Jackson and Buss, 1975), *W. subtorquata* use of space represents exploitative competition as it significantly depletes the use of this resource for *C. foliata* (see Menge, 1995)

Interactions between NIS, where one or both benefit from facilitative interactions have been commonly observed (Simberloff and Von Holle, 1999; Ricciardi, 2001; Floerl et al., 2004). Settlement assays of *W. subtorquata* in the presence of antifouling biocides have reported that *W. subtorquata*'s external surface acts as a non-toxic refugium for sessile epibiotic taxa that are less tolerant and unable to colonise surrounding areas. This has been hypothesised to facilitate the invasions of other species (Floerl et al., 2004; Piola and Johnston, 2006a). This may be accurate, however in this study, the native common encrusting species (*C. foliata*) actively avoided using *W. subtorquata* as a refuge.

Test larvae of the arborescent bryozoans reacted very differently to the test larvae of the encrusting species, especially when compared to control test substrates. Settlement was lower on bare space with no other living organisms present than settlement on bare space adjacent to living substrates (test substrates) (Figure 5.4A and B). More larvae were observed settling on the top of the glass (versus the bottom of the glass) on control substrates, whereas they settled on the bottom of the glass when another species was present. Settlement on the top of glass slides was treated as larval mortality as this does not represent suitable cryptic environments explained by Jackson (1977).

The upright, three-dimensional structure of the arborescent species means they may have less competition for space than the encrusting forms. Arborescent species only occupy a

small amount of substrate in comparison to encrusting forms and overgrowth by encrusting species only occurs at the base, hence they do not undergo the same competition for space as encrusting forms. Grosberg (1981) suggests that a sessile invertebrate species ability to compete, relative to others, influences habitat choice. Grosberg's (1981) empirical research determined different contact interactions with *Botryllus schollosseri* (a dominant overgrowth 'winner'). This researcher's results included three *Bugula spp,* contact interactions for these species resulted in no loss to the arborescent *Bugula spp*. The settlement ratio of arborescent bryozoans within (Chapter 5) acting as epibionts did not vary significantly across different basibiont species although the NIS (*B. neritina*) did settle on native basibionts in greater numbers that NIS basibionts (Figure 5.8A and B).

It was hypothesised at the start of this chapter that; native species will have greater epibiotic pressure than NIS (H9). Species tested within this project showed a strong preference to settle on native species but avoid NIS (Figure 5.5A), suggesting that NIS have a competitive advantage in the form of less epibiotic settling pressure, thus supporting the hypothesis. Additionally it was hypothesised that; native species will show increased preference to settle on native species over settlement onto NIS (H11). Results support this hypothesis as native species did show a preference to settle on native species and seemed to avoid NIS

Results within this chapter infer a modified "release from enemies" interaction is occurring. The release from enemies theory has gained support through research focussed on parasites and predators that are "enemies" (Keane and Crawley, 2002; Torchin et al., 2003; Torchin and Mitchell, 2004). The observed reduction in epibiosis, which may have

deleterious effects, supports a concept of a release from natural enemies (or epibiotic release). Although not definitive, as the epibiotic load of NIS within their native regions has not been determined, this study does provide clear evidence that there is a reduction in epibionts between natives and NIS, which may correlate to reduce harm. Hence, the assumption that native species are subjected to a greater level of epibiotic pressure is strengthened in this study as the native species tested in this settlement assay have significantly greater epibiotic loads than their NIS counterparts.

I hypothesised that; NIS will settle on native species, bare space and NIS at similar frequencies (H10). In contrast to native larvae settlement trends, NIS settled on native species at around the same ratios as settlement onto control substrates, whilst actively avoiding settlement onto NIS species (Figure 5.5B). This finding suggests that NIS see both space occupied by natives and bare space as being free, however here they do not recognise NIS as substrate. This settlement filter of seeing native species as bare space, thus overcomes one of the biggest limiting resources for benthic sessile species: space (Jackson, 1977).

Co-evolution and its ability to explain how negative interactions exists and persist between competitors has been the subject of intense debate for decades (Connell, 1980; Taper and Case, 1992). If the observed epibiotic settlement is to be attributed to co-evolution then it would be presumed that basibiont defence would be greater and as such recruitment onto basibionts would not outweigh that of recruitment onto the control substrates (Connell, 1980). Substrate recognition and a preference to settle on substrates with specific characteristics has been used to explain planktonic recruitment (McKinney and McKinney, 2002; Harrington et al., 2004; Vermeij, 2005; Tyrrell and Byers, 2007), and is one of the driving forces behind the

argument that artificial structures within coastal areas facilitate the successful establishment of NIS (Connell and Glasby, 1999; Glasby et al., 2007).

Epibiosis on *S. unicornis* and *W. subtorquata* was rare within this study in contrast to previously published research. Studies have shown that with the presence of chemical toxins, epibiosis on *W. subtorquata* is increased (Floerl et al., 2004; Piola and Johnston, 2006a, b). However, in an undisturbed environment (i.e., one lacking artificially added toxins) preference to settle on bare space far outweighed epibiotic settlement on *W. subtorquata* in this study (Figure 5.6). Settlement of epibionts on basibiont species showed that the two native basibionts had higher ratios of settlement than the NIS (Figures 5.6), thus reinforcing the theory posited within this thesis that native species are subjected to greater epibiotic loads. Of interest, was the observation of high intraspecific epibiosis where native species showed a preference to settle on adult colonies of the same species at greater densities than what was recorded on the control substrate.

Although recruitment of *C. bispinata* onto adult conspecifics has not been explored within the literature, this phenomenon may be explained by *C. bispinata's* multi-lamellar colony form. *Celleporaria bispinata* takes advantage of limited space by repeatedly overgrowing itself, which enables it to proliferate in spatially restricted environments (Hageman et al., 2003). Recruiting onto adult conspecifics has been recorded in a number of *Celleporaria* species and occurs to the extent where a colony can fully encapsulate their original substrate to form free-living structures called ectoproctaliths or bryoliths (Hara, 2001; Hageman et al., 2003). Barnes and Dick (2000) found intraspecific interactions to be rare whilst illustrating trends in overgrowth competition. However, results of interactions of

20 different species showed that *Celleporaria* sp. had the highest number of overall intraspecific interactions.

The overall larval mortality of natives on control substrates and on substrates where test species were present was significantly greater than the larval mortality of NIS (Figure 5.10). The main implication of reduced larval success is that there is a lower abundance and biomass of native competitors. Observations comparing native and NIS invertebrate larval mortality are uncommon in the literature and as such only broad inferences can be made to why this outcome has been observed. A compensatory release explains that with a reduction in the need for defence, species can reallocate efforts elsewhere. An increased fitness in NIS larvae is considered a competitive advantage for NIS and would support a compensatory release concept. Yet, future work is needed to analyse larval mortality within an invaders native range to support the concept that compensatory release is occurring.

Variations in larval settlement can be attributed to factors such as currents, light, wind patterns and substrate topography (Rodriguez et al., 1993). Much like the primary substrate topography, individuals that live as epibionts also have been shown to show preference when choosing a settlement site based on the microtopography of the underlying species (Ryland, 1974). One reason for the difference observed in epibiotic settlement within this chapter could be on the basis of the morphological shape/structure of the species used in this experiment. It is acknowledged that in part results are confounded in that they are unable to illustrate if this was the case, however results do illustrate that the difference between native and NIS still exists

One major issue that arises with research that examines the differences between success of native species in contrast to the success of an invader is the assumption that both species have had the same opportunity to succeed. The research presented here controlled for a majority of factors that have been hypothesised to affect the successful settlement of marine invertebrate larvae, such as currents (Rittschof et al., 1984), light (Keough and Downes, 1982) and biofilms (Wieczorek and Todd, 1997). Thus by removing much of the variability I have been able to observe the direct consequences NIS have on the settlement of native species. Additionally controlling the aforementioned factors has improved findings as difference in settlement of native and NIS is a function of the presence of a competing species not differing environmental conditions.

CHAPTER 6.
SYNTHESIS

6.1 Summary

Within the literature a number of theories exist surrounding what facilitates invasion success for species. No one theory is representative of all species and in particular for marine species a number of aspects have yet to be explored. In this context, this thesis explored epibiosis as a factor that facilities the invasion success of NIS. This is one of the first efforts to focus on different aspects of epibiosis and discuss these as factors that facilitate successful NIS invasion. Epibiosis can be deemed to be a form of direct competition for many benthic encrusting organisms. Theoretically, a reduction in a regulating factor such as epibiosis would infer an advantage to a species. Conversely having the ability to become an epibiont would confer competitive advantage. These two concepts have led me to explore the epibiont/basibiont association in an effort to elucidate factors that may aid the success of an invasion.

The chapters of this dissertation collectively provide multiple lines of evidence that NIS benefit from reduced epibiosis as basibionts (Chapter 2), that NIS are opportunistic settlers utilising epibiosis when bare space is unavailable (Chapter 4), and that when acting as epibionts NIS remove themselves from competitive interactions (Chapter 5). In doing so, I have provided a theoretical background, made observations on assemblages grown *in situ*, and provided empirical evidence to the fundamental differences that enable the success of NIS compared to native species.

Our theoretical understanding of competing species suggests that native species in the presence of native enemies will have evolved defensive mechanisms to reduce the regulating effects of co-evolved enemies (Torchin et al., 2002; Wolfe, 2002; Roy, 2011). In Chapter 2, a systematic analysis of peer-reviewed research was used to reveal a statistical association between native and NIS epibionts and their settlement onto native or NIS basibionts. More specifically in chapter 2, the systematic review revealed that, on a global scale, native epibionts are found to settle more on native basibionts (and less on NIS basibionts) than what would be expected if settlement was random. Likewise, NIS epibionts were shown to live more on NIS basibiont than expected (and less on native basibionts).

This association was present for data analysed for all benthic species of basibiont (Figure 2. 2), invertebrate basibionts (Figure 2. 3) and analysis of just bryozoan basibionts (Figure 2. 4). Analysis of NIS epibiont/basibiont interactions complemented finding within this chapter, by revealing pairs with species originating from the same bioregion occurred twice as often as pairs where the two species originated from different bioregions (section 2.3.4). Results infer that these NIS show similar preference as natives, choosing to settle on basibiont to whom they share an evolutionary history.

Although many epibiont/basibiont pairs were found during the systematic analysis of the literature, the results from these publications were generally observations made on a single or a few species (often species with commercial interest (Reise, 1998) or invasive species (Bégin and Scheibling, 2003), as opposed to whole communities. Moreover the age of the studied communities and/or substrate type was often different for different studies or not recorded. Thus, comparisons within the literature were fraught with difficulties. Hence, a set

of experiments were designed to examine epibiosis at a community level, using artificial substrates and controlling for time. The results of these experiments were presented in Chapters 3 and 4.

Sessile marine invertebrates have complex life histories that often include a planktonic larval phase. Demography is often attributed to recruitment of larvae, where resumption of benthic stage takes place after metamorphosis (Pawlik, 1992; Tyrrell and Byers, 2007). Monthly observations of recruitment on test substrates over a year illustrated that NIS generally recruit in higher numbers compared to native species. Additionally, the recruitment period of many of the NIS recorded spanned more months than their native competitors (Chapter 3).

Fluctuations in species composition and density are often discussed as a response to varying levels of recruitment and, as such, populations are perceived as being recruitment limited (Hughes, 1990). An important observation made during this study was that recruitment did not equate to species composition and dominance on bare space when bare substrate was limited (Chapter 3). This was particularly evident on artificial settlement plates that were deployed for 6 months, where settlement space was limited due to a dominant species (*Molgula ficus*). Three month treatments deployed for the periods of October to December (austral spring to early summer) and January to March (austral summer and early autumn) had statistically greater amounts of NIS recruits than native species recruits; however six month treatments deployed for some or even all of the same months had statistically greater native species recruitments (Chapter 3). Although the scope of this research did not involve focusing on why this shift in dominance occurred (e.g. predation,

disturbances or competition), it was observed that the native ascidian, *Molgula ficus,* became dominant and that this species contributed to the majority of the overall biomass on the artificial settlement substrate (Chapter 3 and 4).

Results of species composition and dominance determined in Chapter 3 posed an important question: are NIS able to remain successful within assemblages that have limited space and/or where they are not the dominant primary space occupiers? And if so, how do they do it? Therefore, in Chapter 4, the preferences for settling on artificial or biogenic substrates were examined by contrasting recruitment phenology with epibiotic settlement. Temporal differences in the intensity of NIS recruiting as epibionts on native and NIS showed that NIS preference to settle on basibionts corresponded with decreased bare space and increased competition. Thus, it would seem logical that, in order to live and maintain a hold within space limited environments, NIS increasingly relied on epibiosis. More specifically, with the availability of space NIS tend to show no real preference with regards to settling on uncolonised space or as epibionts. However preference changes to settling as basibionts, when bare space becomes limited.

Over half of the NIS recorded recruiting onto bare space were bryozoans. The literature suggests that competitive interactions between ascidians and bryozoans almost always favours ascidians (Gordon, 1972). It was observed that *Molgula ficus* seems to be a gregarious species, with individuals growing tightly together and therefore restricting growth, if not killing, most of the encrusting bryozoans that had once occupied bare space (Chapter 3).

Spatial competition in benthic communities means overgrowth (Jackson, 1977, 1979). However, epibiosis enables adequate substrate for settlement, whilst providing refuge from

competition (overgrowth). It was originally hypothesised that native basibionts would have adapted defence mechanisms against co-evolved native epibionts and as such native epibionts will not show a preference to recruit on them, this however was not supported by the results. In contrast to this, Chapter 2 (results of the systematic analysis) and results from Chapter 3 and 4 indicate that native species showed a strong preference to settle on native basibiont compared to bare space.

Native species preferences to settling on NIS basibionts was significantly lower than their preference to settling on native species. The results in Chapters 4 clearly demonstrate that native species showed a strong preference to settle on native species and bare space but avoided settlement on NIS. NIS have occupied their new marine environments for a brief period of time relative to the evolutionary history of native species with whom they compete (Torchin et al., 2003; Roy, 2011). Substrate forming (human transferred) NIS represent an anthropogenically altered environment that is foreign in regards to the evolutionary history of native.

The cost of epibiosis is different between species (Wahl, 2010). For the majority of marine species, their external bodies have evolved to perform critical functions (Wahl, 1989). These functions include the exchange of substances such as waste products, nutrients and small ions (Wahl, 1989; Wahl, 2010). Furthermore, the external surface or morphological features of many marine species have evolved to combat or utilise hydrodynamic forces such as drag, lift and propulsion (Wahl, 1996). External surface features, such as colour and morphology, have also been shown to affect predator and prey interactions (Cerrano et al., 2001) as well as facilitate reproduction (Green, 1974; Stirnadel and Ebert, 1997; Wahl, 2010).

The external surface of *Molgula ficus* was the most commonly used biogenic substrate within this study (Chapter 4). Although many basibionts incur costs due to epibiosis, epibionts did not seem to affect the success of *Molgula ficus* in this study. Previous research suggests that unless epibionts cover siphons, growth on the thick tunic of solitary ascidian is likely to have minimal to no effect (Gordon, 1972; Claar et al., 2011).

Competition between encrusting bryozoans for space is common, with the outcome of competition generally resulting in the mortality of one of the competitors as a result of being overgrown. Additionally, the calcareous external surfaces of bryozoans offer a hard substrate that that can be exploited as a substrate to grow upon. Given that mortality is the most likely consequence to a losing competitor of overgrowth (Buss, 1979; Jackson, 1979), the ability for a species to remove itself from such competition (settling as an epibiont on top of a competitor) would infer a competitive advantage to the epibiont species. Bryozoans epibionts settling on bryozoan basibionts are not uncommon; to the contrary, such interactions have been commonly reported (Floerl et al., 2004; Stachowicz and Byrnes, 2006). Unfortunately, such a direct interaction was rare within this study (Chapter 4). Therefore, to further assess bryozoan epibiont/basibiont interactions, a manipulative experiment was undertaken; the experiment allowed for propagule pressure and propagule arrival time to be controlled (Chapter 5).

Several studies have shown some bryozoans search and actively choose adequate settlement sites. For example, Keough and Downes (1982) have demonstrated that the presence of a potential competitor may affect the settlement of some species. In Chapter 5, I have specifically demonstrated that the presence of the NIS bryozoan *Watersiporia*

subtorquata impacted the settlement of two of the test larvae species: the native *Celleporaria bispinata*, which had decreased settlement compared to control substrates, and the NIS *Cryptosula pallasiana*, which had increased settlement.

Complementing findings in Chapters 2 and 4, native species examined during the manipulative experiment showed a preference to settle on native species compared to bare space, but preferred bare space over settlement on NIS. NIS larvae settled on native species in similar rates to bare space control substrate (Chapter 5, figure 5.5B), however, like native species, they also avoided settlement onto the NIS test colonies. Thus, it would appear that NIS bryozoan colonies had reduced epibiotic pressure compared to native bryozoan competitors. Epibiosis represents a regulating factor as mortality is often the consequence of being colonised (Buss, 1979; Jackson, 1979; Buss, 1990), similar interactions resulting in a reduction of a regulating factor are generally discussed in the context of enemy release (Wolfe, 2002).

6.2 Future directions

I have hypothesised throughout this dissertation that epibiosis is a factor that facilitates the success of NIS (Jackson, 1977, 1979; Barnes and Dick, 2000). I have discussed success in two different contexts; firstly that epibiosis generally has negative impacts for basibiont hosts and secondly that epibiosis provides substrate and removes a species from competitive interactions. The research within this dissertation has provided important insight to possible mechanisms that facilitate the invasion success if NIS.

This dissertation has generated as many questions (if not more) than have been answered. The evidence suggests that NIS escape natural enemies (i.e., epibionts) from their

native range, which in part explains increased fitness and success compared to native competitors. As such, future studies to assess if NIS have fewer epibionts in invaded regions than in their native region would provide a foundation to understand epibiotic load. Thus, determining if NIS are successful within invaded habitats as they have left co-evolved enemies behind (epibionts) (Torchin et al., 2003). The scope of this dissertation did not include determining the outcome of overgrowth competitive interactions between species (e.g. if the outcome of space competition is in favour of native) yet, it is obvious that determining such outcomes would strengthen the theory that settling on top of a species provides a long term competitive advantage by removing an epibiont from potential competition and possible mortality due to overgrowth. Similarly, the ultimate outcome of epibiosis on the basibiont would provide additional measures of impact.

Species used within the manipulative experiment illustrated the differences in epibiotic pressure and settlement strategies of native and NIS. Species were chosen due to their availability and although there is a vast variety of bryozoan species within Tasmania finding colonies of bryozoans that were reproductively active was difficult. As such future studies expanding on findings within Chapter 5 would be beneficial.

NIS are rarely eradicated (Keller et al., 2007) and this is especially true in the marine environment (Critchley et al., 1986; Bax et al., 2001; Hewitt and Campbell, 2007). Therefore, prediction of potential invaders is of economic and environmental importance (Hewitt and Hayes, 2002; Hewitt et al., 2007). The findings within this dissertation have yielded valuable data on a trait that infers a competitive advantage to species: epibiosis. Future research into

epibiosis may result in a better understanding of which species are likely to become future invaders.

6.3 Conclusions

Many researchers have placed an emphasis on identifying characteristics that facilitate both the initial success of NIS as well as their subsequent establishment and spread. This knowledge would prove extremely useful to both researchers and managers and hence the pursuit of this knowledge is important and is what has driven my researcher to date. The four research chapters presented in this dissertation theoretically, empirically applied ecological data to determine if there are differences in epibiotic pressure for native and NIS and to examine epibiotic preferences between native and NIS.

Successful substrate recognition followed by settlement and growth is a trait considered to be highly selected for among encrusting species, with substrate type likely to hold the greatest influence (Tyrrell and Byers, 2007). The systematic review and experiments conducted within this dissertation clearly demonstrate that on a global (Chapter 2) and local scale (Chapters 4 and 5) that native species show a preference to settle on native species and avoid settling on NIS. This trend has been shown to exist across all benthic invertebrate species where epibiosis is hypothesised to come at a cost to basibionts. Additionally, I have shown that this trend also exists between encrusting bryozoans where consequences of epibiosis generally involve mortality of the underlying species (Chapter 5).

NIS studied within this dissertation exhibited opportunistic settlement characteristics as they viewed all space (bare, native species and NIS to a lesser degree) as freely available. Preference, however, shifted to settling as epibionts with increased competition and

decreased bare space for settlement. Since marine assemblages are generally space limited and subjected to intense competition (Paine, 1974; Jackson, 1977), colonisation of other organisms may be the only successful strategy for survival. Yet, this comes at a cost to the basibiont.

NIS examined throughout this dissertation experienced reduced epibiotic pressure compared to native competitors. An escape from natural enemies is a frequent explanation that is given for the success of NIS (Torchin et al., 2003). Although epibiotic pressure of NIS within their native range is not examined here, this phenomenon does support the theory that species experience less regulation from co-evolved epibionts when they are moved to new geographic locations. Moreover, it has been demonstrated that the choice to settle on a competing species removes an epibiont from overgrowth interactions. The research presented here clearly shows that native species remove themselves from such competition by settling as epibionts on native competitors. NIS remove themselves from similar competitive interactions by settling on both native and NIS and as such are more flexible in the substrates they can utilise.

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APPENDIX A: BIBLIOGRAPHY

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APPENDIX B:
SUPPLEMENTARY MATERIALS FOR CHAPTER 3

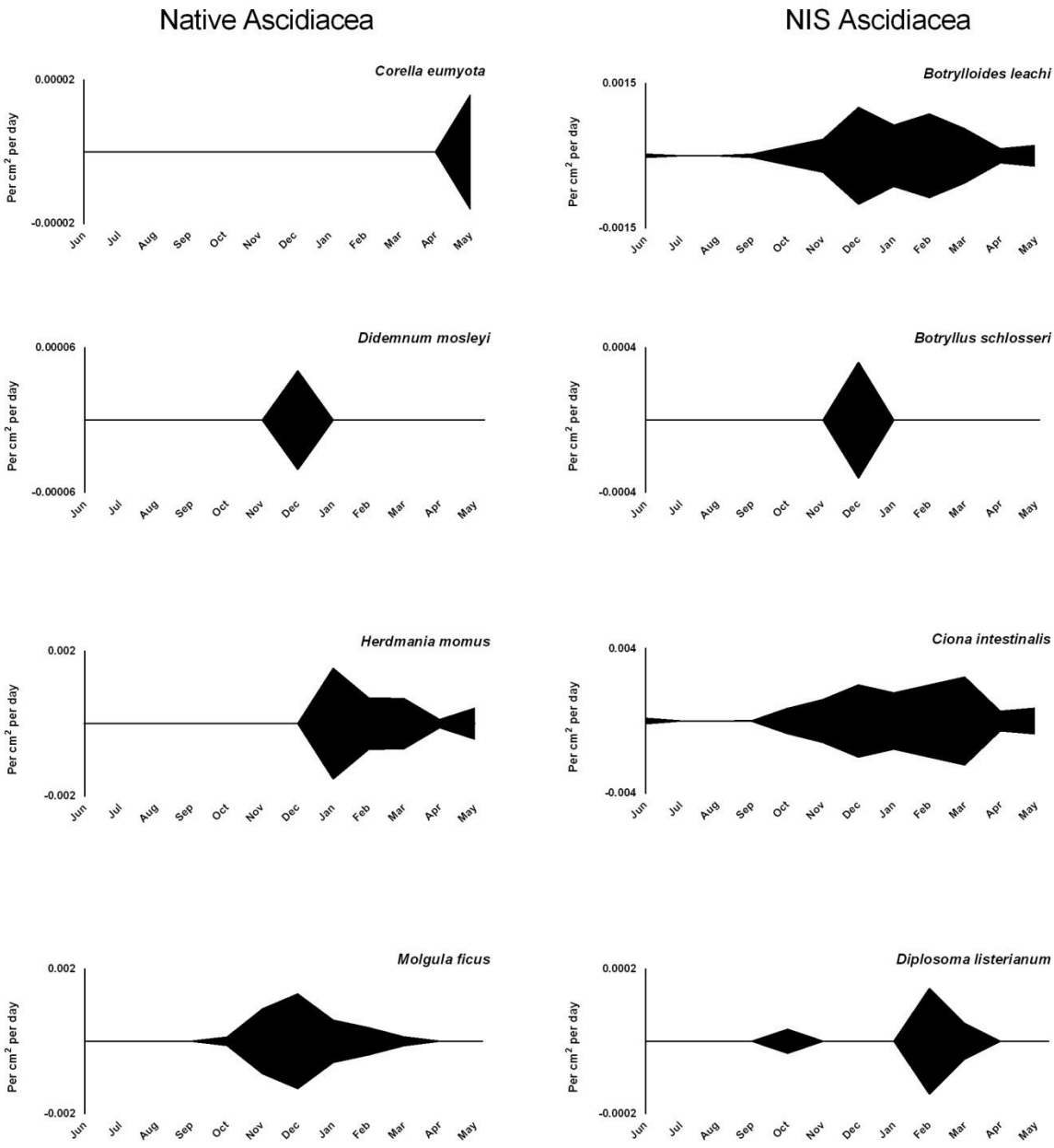

Figure B.1: Kite diagrams depicting the density and duration of recruitment for individual species

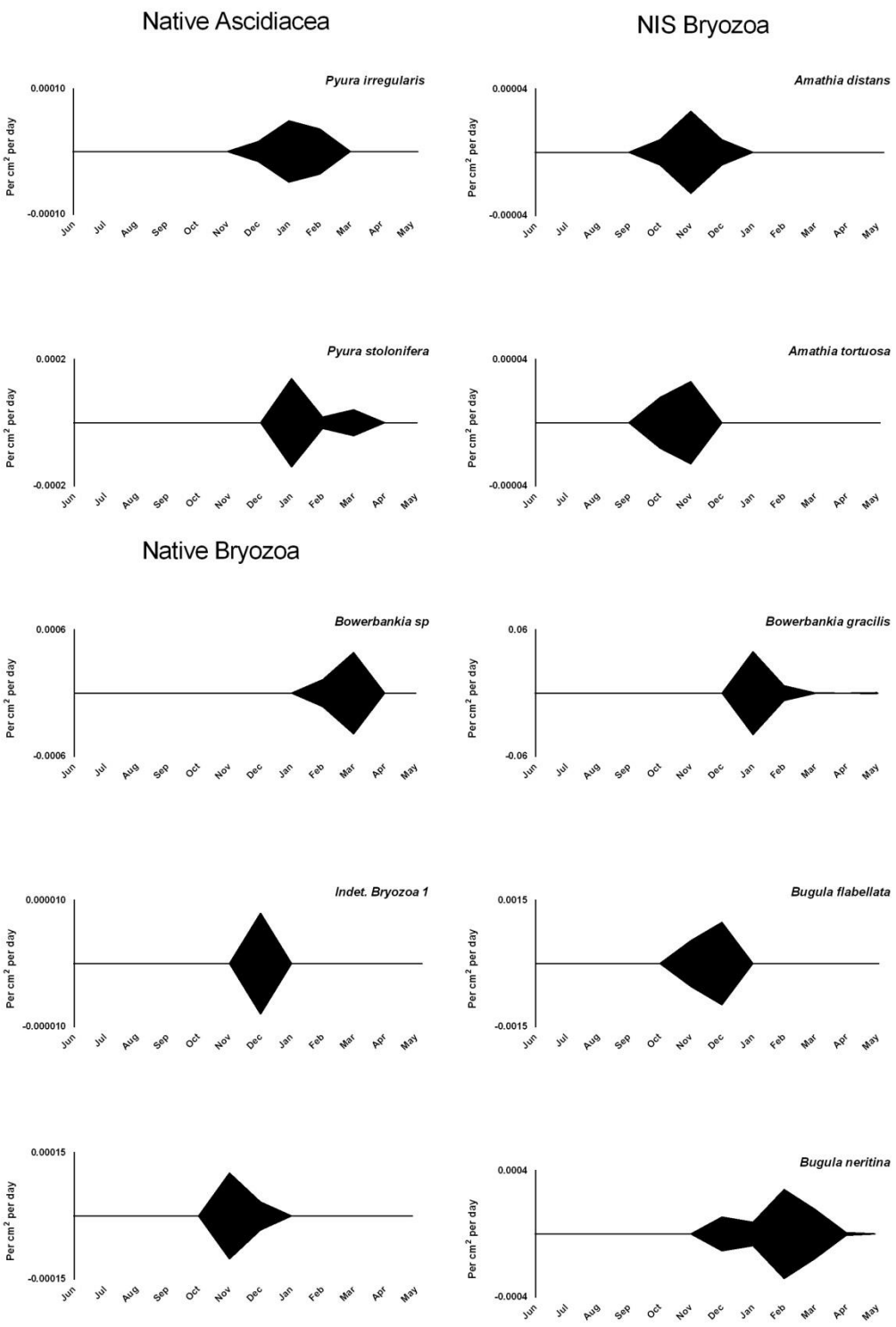

Figure:B.2: Kite diagrams depicting the density and duration of recruitment for individual species

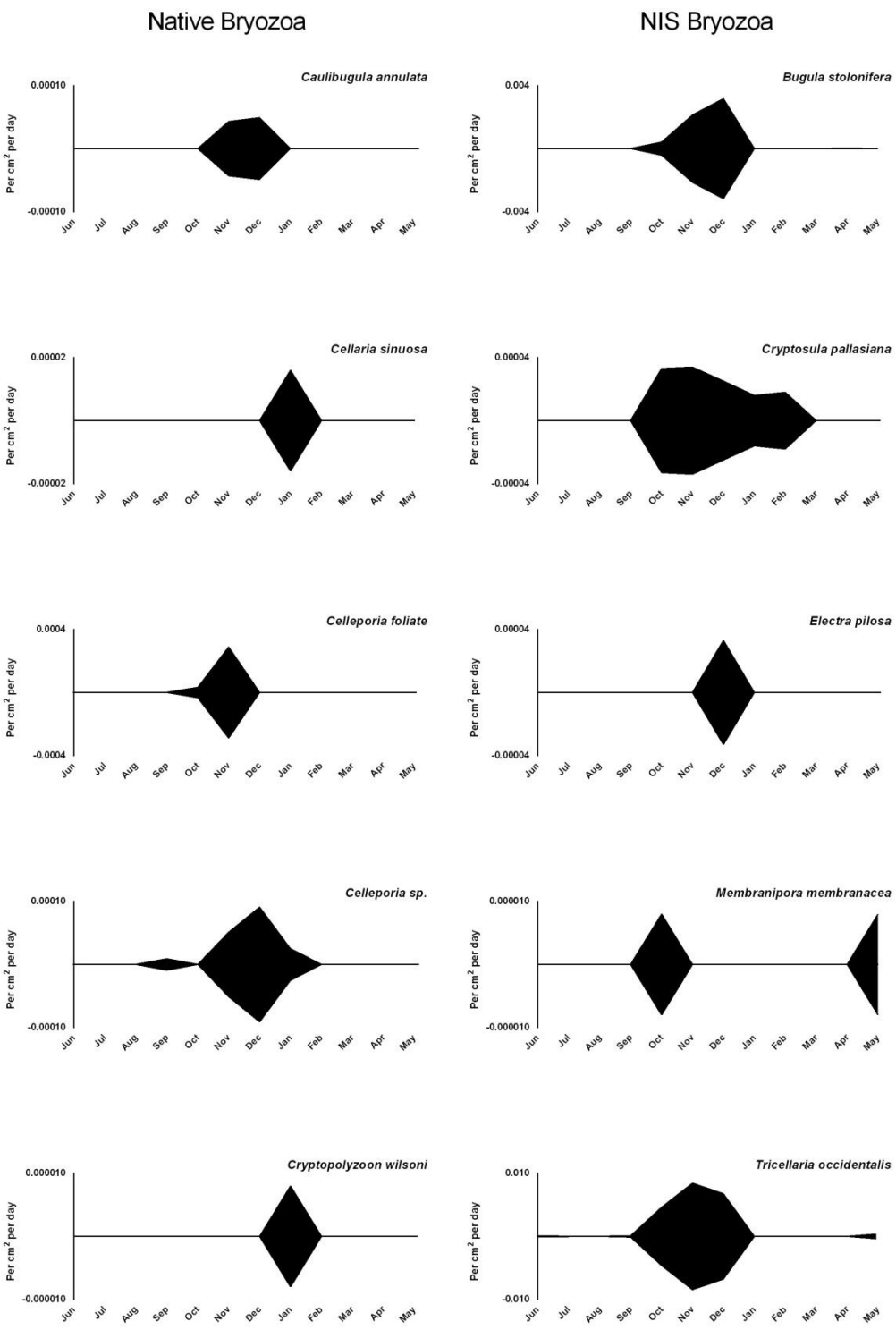

Figure: B.3: Kite diagrams depicting the density and duration of recruitment for individual species

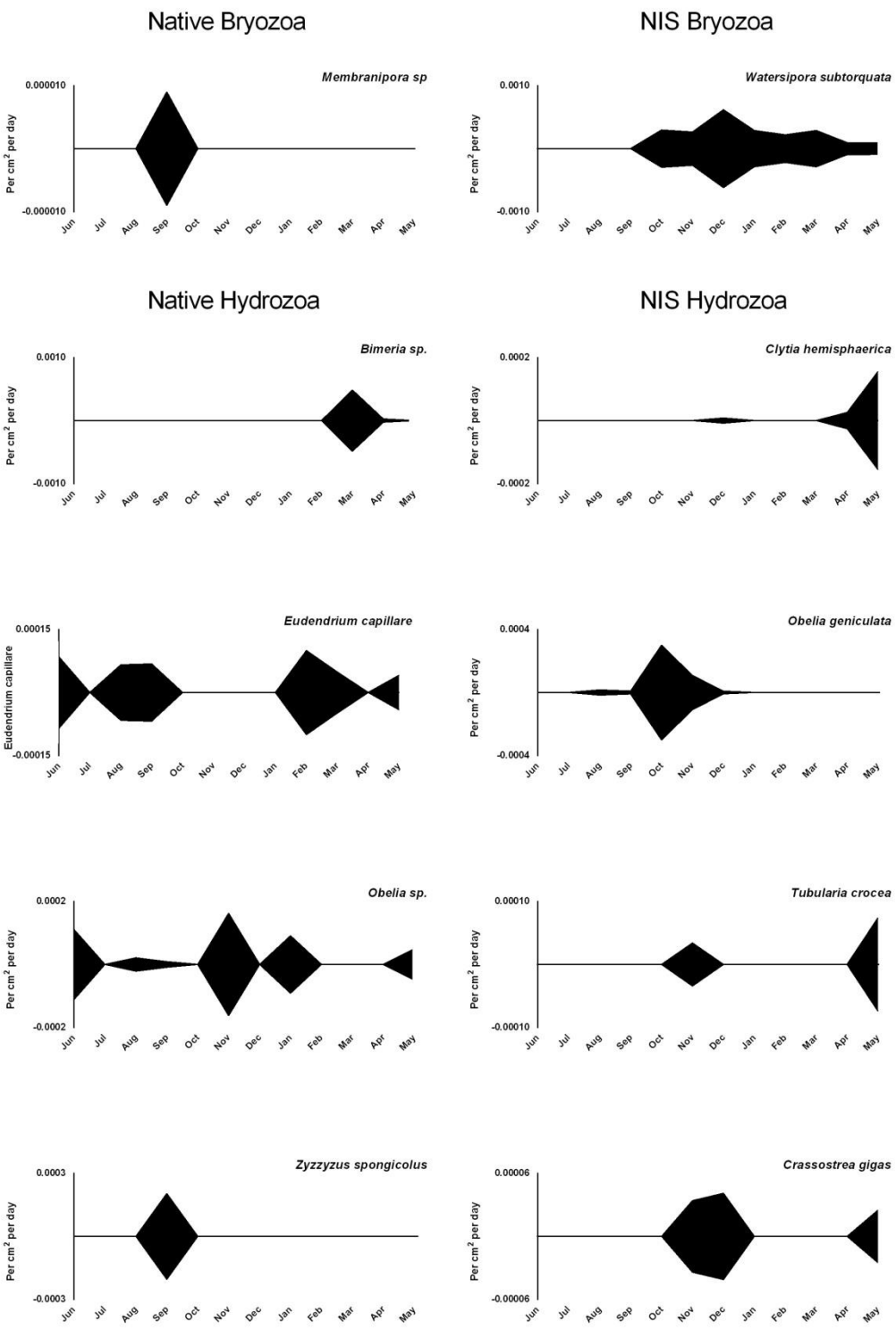

Figure: B.4: Kite diagrams depicting the density and duration of recruitment for individual species

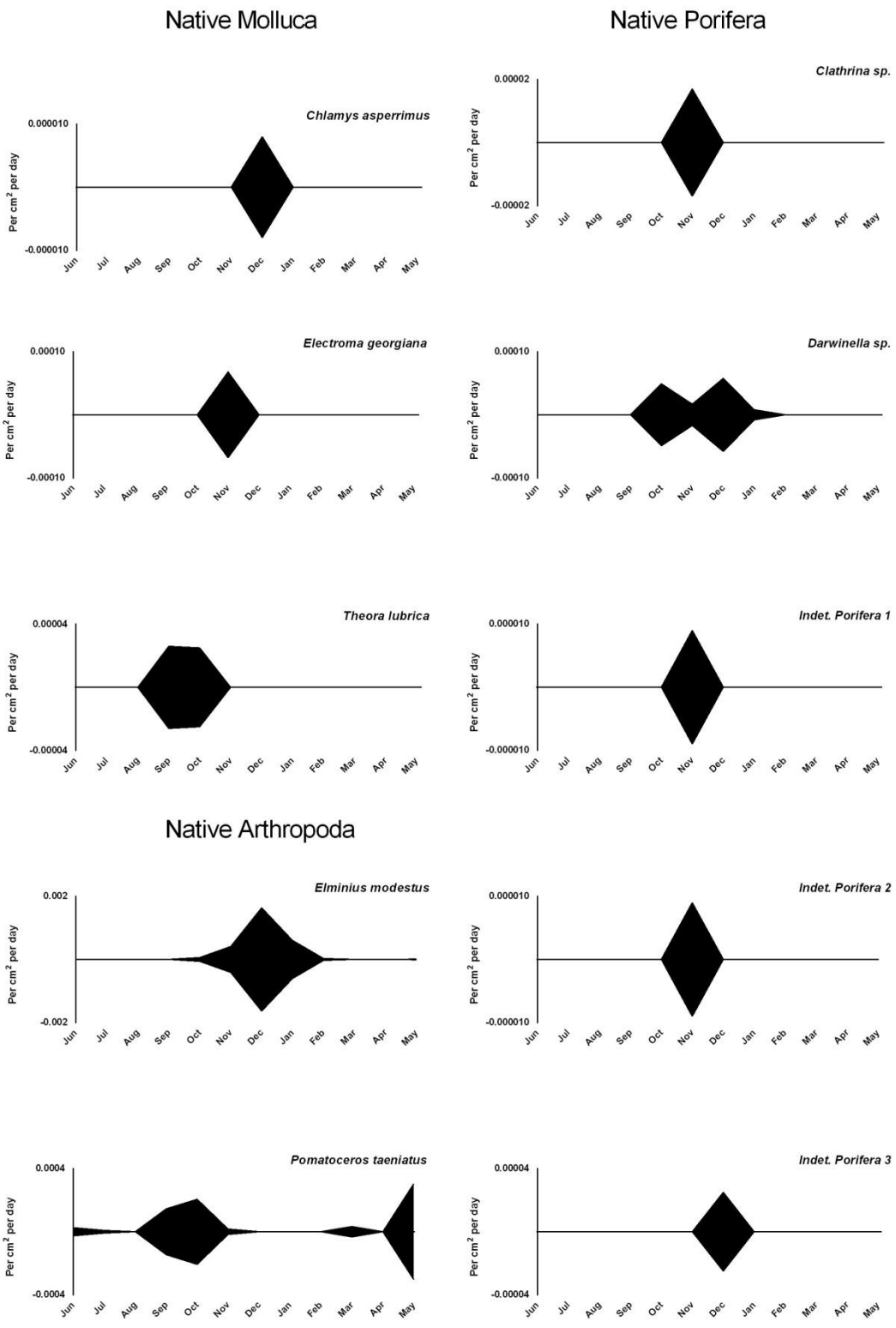

Figure:B.5: Kite diagrams depicting the density and duration of recruitment for individual species

APPENDIX C:

DUNN'S AND TUKEY'S POST HOC TEST VALUES FOR CHAPTER 3

Please note: All p values reported within Appendix C, D and E are Multiplicity adjusted p values (family-wise significant level), as reported by Graphpad 6.0

Table C.1: Tukey's p values for (Figure 3.3). Recruitment of sessile and sedentary species across individual months.

Species status	Month	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
All	**Jun**											
	Jul	>0.9999										
	Aug	>0.9999	>0.9999									
	Sep	>0.9999	0.9994	>0.9999								
	Oct	0.5302	0.2667	0.352	0.8175							
	Nov	**0.002**	**0.0004**	**0.0007**	**0.0093**	0.6322						
	Dec	**0.0001**	**<0.0001**	**<0.0001**	**0.0006**	0.1806	0.9998					
	Jan	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**				
	Feb	0.0688	**0.0204**	**0.0322**	0.2005	0.9976	0.9943	0.7909	**<0.0001**			
	Mar	0.9813	0.8712	0.9272	0.9995	0.9981	0.1082	**0.0123**	**<0.0001**	0.7209		
	Apr	>0.9999	>0.9999	>0.9999	>0.9999	0.444	**0.0012**	**<0.0001**	**<0.0001**	**0.0488**	0 .9625	
	May	>0.9999	0.9975	0.9994	>0.9999	0.8848	**0.0148**	**0 .0011**	**<0.0001**	0.2682	>0.9999	>0.9999
Native	**Jun**											
	Jul	>0.9999										
	Aug	>0.9999	>0.9999									
	Sep	>0.9999	>0.9999	>0.9999								
	Oct	0.3522	0.2966	0.2994	0.7217							
	Nov	**0.0073**	**0.0052**	**0.0053**	**0.0407**	0.9487						

Species status	Month	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
	Dec	**0.0008**	**0.0006**	**0.0006**	**0.006**	0.6534	>0.9999					
	Jan	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**				
	Feb	0.0804	0.0623	0.0631	0.2797	>0.9999	0.9997	0.9634	**<0.0001**			
	Mar	0.996	0.9917	0.992	>0.9999	0.9508	0.1542	**0.0309**	**<0.0001**	0.6121		
	Apr	>0.9999	>0.9999	>0.9999	>0.9999	0.4619	**0.0127**	**0.0015**	**<0.0001**	0.1231	0.9992	
	May	>0.9999	0.9998	0.9998	>0.9999	0.7913	0.0563	**0.0088**	**<0.0001**	0.345	>0.9999	>0.9999
NIS	**Jun**											
	Jul	0.8288										
	Aug	0.9978	0.9997									
	Sep	>0.9999	0.9772	>0.9999								
	Oct	0.9978	0.9997	>0.9999	>0.9999							
	Nov	0.2209	**0.001**	**0.0157**	0.0713	**0.0157**						
	Dec	**0.0196**	**<0.0001**	**0.0006**	**0.004**	**0.0006**	0.9989					
	Jan	**0.0321**	**<0.0001**	**0.0011**	**0.0071**	**0.0011**	0.9998	>0.9999				
	Feb	0.9989	0.2473	0.759	0.9641	0.759	0.7991	0.2215	0.3044			
	Mar	0.9762	0.1003	0.489	0.8251	0.489	0.9544	0.4521	0.5645	>0.9999		
	Apr	0.9178	>0.9999	>0.9999	0.9944	>0.9999	**0.0021**	**<0.0001**	**0.0001**	0.3646	0.1655	
	May	>0.9999	0.9444	>0.9999	>0.9999	>0.9999	0.1113	**0.0073**	0.0126	0.9869	0.9025	0.9816

Table C.2: Dunn's p values for (Figure 3.4) Recruitment of individual native and NIS recorded for June.

	T occidentalis	***C intestinalis***	***B leachi***	***P taeniatus***	***Obelia sp 1***
C intestinalis	>0.99				
B leachi	>0.99	>0.99			
P taeniatus	>0.99	>0.99	>0.99		
Obelia sp 1	>0.99	>0.99	>0.99	>0.99	
E capillare	**0.005**	**0.046**	**<0.001**	**<0.001**	**0.012**

Table C.3: Dunn's p values for (Figure 3.6). Recruitment of individual native and NIS recorded for August.

	O geniculata	***Obelia sp 1***	***E capillare***
O geniculata			
Obelia sp 1	>0.99		
E capillare	**0.042**	**0.0226**	

Table C.4: Dunn's p values for (figure 3.7). Recruitment of individual native and NIS recorded for September.

	T occidentalis	***O geniculata***	***C intestinalis***	***B leachi***	***Z spongicolus***	***T lubrica***	***P taeniatus***	***Obelia sp 1***	***Membranipora sp***	***E capillare***	***Celleporia sp.***
T occidentalis											
O geniculata	0.426										
C intestinalis	>0.99	**0.004**									
B leachi	>0.99	0.065	>0.99								
Z spongicolus	>0.99	0.707	>0.99	>0.99							
T lubrica	>0.99	**0.017**	>0.99	>0.99	>0.99						
P taeniatus	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99					
Obelia sp 1	>0.99	**0.008**	>0.99	>0.99	>0.99	>0.99	>0.99				
Membranipora sp	>0.99	**0.003**	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99			
E capillare	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99		
Celleporia sp.	>0.99	**0.003**	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	

Table C.5: Dunn's p values for (Figure 3.8). Recruitment of individual native and NIS recorded for October.

	W subtorquata	*T occidentalis*	*O geniculata*	*M membranacea*	*D listerianum*	*C pallasiana*	*C intestinalis*	*B stolonifera*	*B leachi*	*A tortuosa*	*A distains*	*T lubrica*	*P taeniatus*	*M ficus*	*E modestus*	*Darwinella sp*	*C foliate*
W subtorquata																	
T occidentalis	**0.002**																
O geniculata	>0.99	>0.99															
M membranacea	>0.99	**<0.001**	0.054														
D listerianum	>0.99	**<0.001**	0.076	>0.99													
C pallasiana	>0.99	**0.001**	0.643	>0.99	>0.99												
C intestinalis	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99											
B stolonifera	>0.99	**0.006**	>0.99	>0.99	>0.99	>0.99	>0.99										
B leachi	>0.99	**0.002**	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99									
A tortuosa	>0.99	**<0.001**	0.178	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99								
A distains	>0.99	**<0.001**	0.054	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99							
T lubrica	>0.99	**<0.001**	0.218	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99						
P taeniatus	>0.99	0.278	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99					
M ficus	>0.99	**0.011**	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99				
E modestus	>0.99	**<0.001**	0.323	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99			
Darwinella sp	>0.99	**0.005**	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99		
C foliate	>0.99	**0.001**	0.687	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	

Table C.6A : Dunn's p values for (Figure 3.9). Recruitment of individual native and NIS recorded for November.

	W subtorquata	*T crocea*	*T occidentalis*	*O geniculata*	*C pallasiana*	*C gigas*	*C intestinalis*	*B flabellata*	*B stolonifera*	*B leachi*	*A tortuosa*	*A distains*	*P taeniatus*	*Obelia sp 2*	*M ficus*
T crocea	>0.99														
T occidentalis	0.364	**<0.001**													
O geniculata	>0.99	>0.99	0.311												
C pallasiana	>0.99	>0.99	**<0.001**	>0.99											
C gigas	>0.99	>0.99	**<0.01**	>0.99	>0.99										
C intestinalis	>0.99	0.782	>0.99	>0.99	0.782	>0.99									
B flabellata	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99								
B stolonifera	>0.99	0.001	>0.99	>0.99	**0.001**	**0.003**	>0.99	>0.99							
B leachi	>0.99	>0.99	0.687	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99						
A tortuosa	>0.99	>0.99	**<0.001**	>0.99	>0.99	>0.99	0.699	0.975	**0.001**	>0.99					
A distains	>0.99	>0.99	**<0.001**	>0.99	>0.99	>0.99	0.699	0.975	**0.001**	>0.99	>0.99				
P taeniatus	>0.99	>0.99	**<0.001**	>0.99	>0.99	>0.99	0.573	0.804	**0.001**	>0.99	>0.99	>0.99			
Obelia sp 2	>0.99	>0.99	**<0.01**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.008**	>0.99	>0.99	>0.99	>0.99		
M ficus	>0.99	**0.023**	>0.99	>0.99	**0.023**	0.061	>0.99	>0.99	>0.99	>0.99	**0.020**	**0.020**	**0.016**	0.128	
Porifera 2	>0.99	>0.99	**<0.001**	>0.99	>0.99	>0.99	0.222	0.319	**<0.01**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.005**
Porifera 1	>0.99	>0.99	**<0.001**	>0.99	>0.99	>0.99	0.222	0.319	**<0.01**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.005**
Bryozoa 1	>0.99	>0.99	**0.005**	>0.99	>0.99	>0.99	>0.99	>0.99	0.082	>0.99	>0.99	>0.99	>0.99	>0.99	0.943
E modestus	>0.99	>0.99	0.300	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
E georgiana	>0.99	>0.99	<0.001	>0.99	>0.99	>0.99	>0.99	>0.99	**0.002**	>0.99	>0.99	>0.99	>0.99	>0.99	0.033
Darwinella sp	>0.99	>0.99	**<0.001**	>0.99	>0.99	>0.99	0.573	0.804	**0.001**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.016**
Clathrina sp	>0.99	>0.99	**<0.001**	>0.99	>0.99	>0.99	0.573	0.804	**0.001**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.016**
Celleporia sp.	>0.99	>0.99	**<0.01**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.004**	>0.99	>0.99	>0.99	>0.99	>0.99	0.078
C foliate	>0.99	>0.99	0.377	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
C annulata	>0.99	>0.99	**<0.01**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.004**	>0.99	>0.99	>0.99	>0.99	>0.99	0.077

Table C.6 B: Dunn's p values for (Figure 3.9). Recruitment of individual native and NIS recorded for November.

	Porifera 2	*Porifera 1*	*Bryozoa 1*	*E modestus*	*E georgiana*	*Darwinella sp*	*Clathrina sp*	*Celleporia sp.*	*C foliate*
Porifera 1	>0.99								
Bryozoa 1	>0.99	>0.99							
E modestus	>0.99	>0.99	>0.99						
E georgiana	>0.99	>0.99	>0.99	>0.99					
Darwinella sp	>0.99	>0.99	>0.99	>0.99	>0.99				
Clathrina sp	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99			
Celleporia sp.	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99		
C foliate	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	
C annulata	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99

Table C.7A: Dunn's p values for (Figure 3.10). Recruitment of individual native and NIS recorded for December.

	W subtorquata	*T ccidentalis*	*O geniculata*	*E pilosa*	*C gigas*	*C hemisphaerica*	*C intestinalis*	*B stolonifera*	*B neritina*	*B flabellata*	*B schlosseri*	*B leachi*	*P stolonifera*	*P irregularis*	*M ficus*
O geniculata	0.705	**<.001**													
E pilosa	>0.99	**0.001**	>0.99												
C gigas	>0.99	**0.001**	>0.99	>0.99											
C hemisphaerica	0.703	**<.001**	>0.99	>0.99	>0.99										
C intestinalis	>0.99	>0.99	0.055	0.634	>0.99	**0.055**									
B stolonifera	>0.99	>0.99	**<.001**	**0.002**	**0.009**	**<.001**	>0.99								
B neritina	>0.99	**0.015**	>0.99	>0.99	>0.99	>0.99	>0.99	0.092							
B flabellata	>0.99	>0.99	0.059	0.680	>0.99	0.059	>0.99	>0.99	>0.99						
B schlosseri	>0.99	**0.001**	>0.99	>0.99	>0.99	>0.99	0.544	**0.002**	>0.99	0.584					
B leachi	>0.99	>0.99	**0.018**	0.2459	0.698	**0.018**	>0.99	>0.99	>0.99	>0.99	.2088				
P stolonifera	>0.99	**<.001**	>0.99	>0.99	>0.99	>0.99	0.174	**0.001**	>0.99	0.188	>0.99	0.061			
P irregularis	0.869	**<.001**	>0.99	>0.99	>0.99	>0.99	0.071	**0.001**	>0.99	0.077	>0.99	**0.023**	>0.99		
M ficus	>0.99	>0.99	**0.003**	0.058	0.185	**0.003**	>0.99	>0.99	>0.99	>0.99	.0491	>0.99	**0.013**	**0.005**	
Spirorbid 1	>0.99	**<.001**	>0.99	>0.99	>0.99	>0.99	0.1748	**0.001**	>0.99	0.188	>0.99	0.061	>0.99	>0.99	**0.013**
Porifera 3	>0.99	**0.001**	>0.99	>0.99	>0.99	>0.99	0.509	**0.002**	>0.99	0.547	>0.99	0.194	>0.99	>0.99	**0.045**
Bryozoa 2	0.96	**<.001**	>0.99	>0.99	>0.99	>0.99	0.086	**0.001**	>0.99	0.086	>0.99	**0.026**	>0.99	>0.99	**0.005**
Bryozoa 1	0.703	**<.001**	>0.99	>0.99	>0.99	>0.99	0.055	**<.001**	>0.99	0.059	>0.99	**0.018**	>0.99	>0.99	**0.003**
E modestus	>0.99	0.341	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
D moseleyi	>0.99	**<.001**	>0.99	>0.99	>0.99	>0.99	0.084	**0.001**	>0.99	0.0913	>0.99	0.028	>0.99	>0.99	**0.005**
Darwinella sp	>0.99	**0.002**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.011**	>0.99	>0.99	>0.99	0.773	>0.99	>0.99	0.207
C pallasiana	>0.99	**<.001**	>0.99	>0.99	>0.99	>0.99	0.221	**0.001**	>0.99	0.238	>0.99	0.079	>0.99	>0.99	**0.017**
C asperrimus	0.703	**<.001**	>0.99	>0.99	>0.99	>0.99	0.055	**<.001**	>0.99	0.059	>0.99	0.018	>0.99	>0.99	**0.003**
Celleporia sp.	>0.99	**0.009**	>0.99	>0.99	>0.99	>0.99	>0.99	0.058	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	0.821
C annulata	>0.99	**0.001**	>0.99	>0.99	>0.99	>0.99	>0.99	**0.011**	>0.99	>0.99	>0.99	0.741	>0.99	>0.99	0.198
A distains	0.707	**<.001**	>0.99	>0.99	>0.99	>0.99	0.055	**<.001**	>0.99	0.059	>0.99	**0.018**	>0.99	>0.99	**0.003**

Table C.7B: Dunn's p values for (Figure 3.10). Recruitment of individual native and NIS recorded for December.

	I Spirorbid 1	*Porifera 3*	*Bryozoa 2*	*Bryozoa 1*	*E modestus*	*D moseleyi*	*Darwinella sp*	*C pallasiana*	*C asperrimus*	*Celleporia sp.*	*C annulata*
Porifera 3	>0.99										
Bryozoa 2	>0.99	>0.99									
Bryozoa 1	>0.99	>0.99	>0.99								
E modestus	>0.99	>0.99	>0.99	>0.99							
D moseleyi	>0.99	>0.99	>0.99	>0.99	>0.99						
Darwinella sp	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99					
C pallasiana	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99				
C asperrimus	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99			
Celleporia sp.	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99		
C annulata	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	
A distains	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99

Table C.8: Dunn's p values for (Figure 3.11). Recruitment of individual native and NIS recorded for January.

	W subtorquata	*T occidentalis*	*C pallasiana*	*C intestinalis*	*B neritina*	*B gracilis*	*B leachi*	*P stolonifera*	*P irregularis*	*Obelia sp 1*	*M ficus*	*Spirorbid 1*	*H momus*	*E modestus*	*Darwinella sp*	*C wilsoni*	*Celleporia sp.*
W subtorquata																	
T occidentalis	>0.999																
C pallasiana	>0.999	>0.999															
C intestinalis	>0.999	**0.001**	**0.001**														
B neritina	>0.999	>0.999	>0.999	0.274													
B gracilis	0.384	< 0.0001	< 0.001	>0.999	**0.007**												
B leachi	>0.999	0.055	0.097	>0.999	>0.999	>0.999											
P stolonifera	>0.999	>0.999	>0.999	**0.018**	>0.999	**0.000**	0.907										
P irregularis	>0.999	>0.999	>0.999	**0.002**	>0.999	**< 0.001**	0.193	>0.999									
Obelia sp 1	>0.999	>0.999	>0.999	**0.011**	>0.999	0.001	0.631	>0.999	>0.999								
M ficus	>0.999	0.270	0.450	>0.999	>0.999	>0.999	>0.999	>0.999	0.828	>0.999							
Spirorbid 1	>0.999	>0.999	>0.999	**0.003**	>0.999	< 0.001	0.238	>0.999	>0.999	>0.999	0.993						
H momus	>0.999	0.062	0.109	>0.999	>0.999	>0.999	>0.999	>0.999	0.216	0.698	>0.999	0.265					
E modestus	>0.999	0.052	0.092	>0.999	>0.999	>0.999	>0.999	0.870	0.184	0.604	>0.999	0.227	>0.999				
Darwinella sp	>0.999	>0.999	>0.999	**0.000**	>0.999	**< 0.001**	0.037	>0.999	>0.999	>0.999	0.192	>0.999	**0.042**	**0.035**			
C wilsoni	>0.999	>0.999	>0.999	**0.000**	>0.999	**< 0.001**	**0.037**	>0.999	>0.999	>0.999	0.192	>0.999	**0.042**	**0.035**	>0.999		
Celleporia sp.	>0.999	>0.999	>0.999	**0.001**	>0.999	**< 0.001**	0.124	>0.999	>0.999	>0.999	0.557	>0.999	0.139	0.118	>0.999	>0.999	
C sinuosa	>0.999	>0.999	>0.999	**0.001**	>0.999	**< 0.001**	**0.097**	>0.999	>0.999	>0.999	0.450	>0.999	0.109	0.092	>0.999	>0.999	>0.999

Table C.9: Dunn's p values for (Figure 3.12). Recruitment of individual native and NIS recorded for February.

	W subtorquata	*D listerianum*	*pallasiana*	*C intestinalis*	*B neritina*	*B gracilis*	*B leachi*	*P stolonifera*	*P irregularis*	*M ficus*	*H momus*	*E capillare*	*E modestus*
W subtorquata													
D listerianum	>0.999												
C pallasiana	>0.999	>0.999											
C intestinalis	0.302	**0.029**	**<0.001**										
B neritina	>0.999	>0.999	>0.999	0.458									
B gracilis	>0.999	>0.999	**0.019**	>0.999	>0.999								
B leachi	>0.999	0.484	**0.003**	>0.999	>0.999	>0.999							
P stolonifera	>0.999	>0.999	>0.999	**<0.001**	>0.999	**0.019**	**0.003**						
P irregularis	>0.999	>0.999	>0.999	**0.000**	>0.999	0.052	**0.009**	>0.999					
M ficus	>0.999	>0.999	>0.999	0.534	>0.999	>0.999	>0.999	>0.999	>0.999				
H momus	>0.999	>0.999	>0.999	0.583	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999			
E capillare	>0.999	>0.999	>0.999	0.210	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999		
E modestus	>0.999	>0.999	>0.999	**0.001**	>0.999	0.083	**0.016**	>0.999	>0.999	>0.999	>0.999	>0.999	
Bowerbankia sp	>0.999	>0.999	>0.999	**0.001**	>0.999	0.155	**0.032**	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999

Table C.10: Dunn's p values for (Figure 3.13). Recruitment of individual native and NIS recorded for March.

	W subtorquata	*D listerianum*	*C intestinalis*	*B neritina*	*B gracilis*	*B leachi*	*P stolonifera*	*P taeniatus*	*M ficus*	*H momus*	*E capillare*	*Bowerbankia sp*	*Bimeria sp*
W subtorquata													
D listerianum	0.638												
C intestinalis	>0.999	**<0.001**											
B neritina	>0.999	>0.999	0.053										
B gracilis	>0.999	>0.999	**0.042**	>0.999									
B leachi	>0.999	0.129	>0.999	>0.999	>0.999								
P stolonifera	0.593	>0.999	<0.001	>0.999	>0.999	0.118							
P taeniatus	0.718	>0.999	<0.001	>0.999	>0.999	0.148	>0.999						
M ficus	>0.999	>0.999	**0.001**	>0.999	>0.999	>0.999	>0.999	>0.999					
H momus	>0.999	**0.012**	>0.999	>0.999	>0.999	>0.999	**0.011**	**0.014**	0.180				
E capillare	>0.999	>0.999	**0.001**	>0.999	>0.999	0.765	>0.999	>0.999	>0.999	0.099			
Bowerbankia sp	>0.999	>0.999	**0.031**	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999		
Bimeria sp	>0.999	>0.999	**0.000**	>0.999	>0.999	0.674	>0.999	>0.999	>0.999	0.085	>0.999	>0.999	

Table C.11: Dunn's p values for (Figure 3.14). Recruitment of individual native and NIS recorded for April.

	W subtorquata	*C hemisphaerica*	*C intestinalis*	*B stolonifera*	*B neritina*	*B gracilis*	*B leachi*	*Herdmania sp*
W subtorquata								
C hemisphaerica	>0.999							
C intestinalis	**0.045**	**< 0.001**						
B stolonifera	>0.999	>0.999	**< 0.001**					
B neritina	>0.999	>0.999	**< 0.001**	>0.999				
B gracilis	>0.999	>0.999	**0.002**	>0.999	>0.999			
B leachi	>0.999	0.305	>0.999	0.082	0.082	>0.999		
Herdmania sp	>0.999	>0.999	0.089	>0.999	>0.999	>0.999	>0.999	
Bimeria sp	>0.999	>0.999	**< 00001**	>0.999	>0.999	>0.999	0.305	>0.999

Table C.12: Dunn's p values for (Figure 3.15). Recruitment of individual native and NIS recorded for May.

	W .subtorquata	*T .crocea*	*T .occidentalis*	*M .membranacea*	*C .gigas*	*C .hemisphaerica*	*C .intestinalis*	*B .gracilis*	*B .leachi*	*P .taeniatus*	*Obelia sp .1*	*Spirorbid .1*	*H .momus*	*E .capillare*	*E .modestus*
W .subtorquata															
T .crocea	>0.999														
T .occidentalis	>0.999	>0.999													
M .membranacea	>0.999	>0.999	>0.999												
C .gigas	>0.999	>0.999	>0.999	>0.999											
C .hemisphaerica	>0.999	>0.999	>0.999	>0.999	>0.999										
C .intestinalis	>0.999	0.183	>0.999	**0.022**	**0.030**	>0.999									
B .gracilis	>0.999	0.980	>0.999	0.154	0.206	>0.999	>0.999								
B .leachi	>0.999	>0.999	>0.999	0.189	0.250	>0.999	>0.999	>0.999							
P .taeniatus	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999						
Obelia .sp .1	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	**0.388**	>0.999	>0.999	>0.999					
Indet .Spirorbid .1	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	**0.022**	0.154	0.189	>0.999	>0.999				
H .momus	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999			
E .capillare	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	0.210	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999		
E .modestus	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	**0.022**	0.154	0.189	>0.999	>0.999	>0.999	>0.999	>0.999	
C .eumyota	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	**0.026**	0.182	0.222	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999

Table C.13: Tukey's p values for (Figure 3.19). Recruitment of sessile and sedentary species for the 3-month settlement treatment for the various species.

		Jul-Sep	Oct-Dec	Jan-Mar
All	Jul-Sep			
	Oct-Dec	**< 0.0001**		
	Jan-Mar	**< 0.0001**	0.4008	
	Apr-Jun	0.0975	**< 0.0001**	**< 0.0001**
Native	Jul-Sep			
	Oct-Dec	0.6514		
	Jan-Mar	0.6764	> 0.9999	
	Apr-Jun	0.9741	0.3971	0.42
NIS	Jul-Sep			
	Oct-Dec	**< 0.0001**		
	Jan-Mar	**< 0.0001**	0.7975	
	Apr-Jun	0.0605	**0.0002**	**< 0.0001**

Table C.14: Dunn's p values for (figure 3.20). Recruitment of individual native species and NIS during the 3-month treatments for different seasons July-September

	B leachi	***O geniculata***	***T occidentalis***	***E modestus***	***E capillare***	***M ficus***	***P taeniatus***
B leachi							
O geniculata	> 0.9999						
T occidentalis	> 0.9999	> 0.9999					
E modestus	> 0.9999	> 0.9999	0.9396				
E capillare	**0.0019**	**0.0238**	0.2177	**< 0.0001**			
M ficus	> 0.9999	> 0.9999	0.9396	> 0.9999	**< 0.0001**		
P taeniatus	> 0.9999	> 0.9999	> 0.9999	> 0.9999	0.1529	> 0.9999	
Z spongicolus	> 0.9999	> 0.9999	> 0.9999	> 0.9999	**0.0238**	> 0.9999	> 0.9999

Table C.15 A: Dunn's p values for (Figure 3.20). Recruitment of individual native species and NIS during the 3-month treatments for different seasons October-December

	W subtorquata	*T occidentalis*	*S unicornis*	*O geniculata*	*D listerianum*	*C pallasiana*	*C gigas*	*C intestinalis*	*B stolonifera*	*B schlosseri*	*B leachi*	*A distans*
W subtorquata												
T occidentalis	>0.999											
S unicornis	>0.999	**0.001**										
O geniculata	>0.999	**0.002**	>0.999									
D listerianum	>0.999	>0.999	>0.999	>0.999								
C pallasiana	>0.999	**0.001**	>0.999	>0.999	>0.999							
C gigas	>0.999	**0.001**	>0.999	>0.999	>0.999	>0.999						
C intestinalis	>0.999	>0.999	**0.002**	**0.002**	>0.999	**0.001**	**0.001**					
B stolonifera	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999				
B schlosseri	>0.999	**0.004**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.005**	>0.999			
B leachi	>0.999	>0.999	**0.002**	**0.002**	>0.999	**0.001**	**0.001**	>0.999	>0.999	0.004		
A distans	>0.999	**0.001**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.002**	>0.999	>0.999	**0.001**	
P irregularis	>0.999	**0.005**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.007**	>0.999	>0.999	**0.005**	>0.999
P taeniatus	>0.999	**0.001**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.001**	>0.999	>0.999	**0.001**	>0.999
M ficus	0.238	>0.999	**<0.001**	**<0.001**	0.235	**<0.001**	**<0.001**	>0.999	>0.999	**<0.001**	>0.999	**<0.001**
Bryozoan 2	>0.999	0.283	>0.999	>0.999	>0.999	>0.999	>0.999	0.366	>0.999	>0.999	0.289	>0.999
Bryozoan 1	>0.999	**0.001**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.001**	>0.999	>0.999	**0.001**	>0.999
E modestus	>0.999	0.065	>0.999	>0.999	>0.999	>0.999	>0.999	0.086	>0.999	>0.999	0.066	>0.999
Celleporaria sp 1	>0.999	**0.019**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.026**	>0.999	>0.999	**0.019**	>0.999
C foliata	>0.999	**0.002**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.002**	>0.999	>0.999	**0.002**	>0.999
C annulata	>0.999	**0.001**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.001**	>0.999	>0.999	**0.001**	>0.999
B flabellata	>0.999	**0.019**	>0.999	>0.999	>0.999	>0.999	>0.999	**0.026**	>0.999	>0.999	**0.019**	>0.999

Table C.15B: Dunn's p values for (Figure 3.20). Recruitment of individual native species and NIS during the 3-month treatments for different seasons October-December

	P irregularis	*P taeniatus*	*M ficus*	*Bryozoan 2*	*Bryozoan 1*	*E modestus*	*Celleporaria sp 1*	*C foliata*	*C annulata*	*B flabellata*
P taeniatus	>0.999									
M ficus	**<0.001**	**<0.001**								
Bryozoan 2	>0.999	>0.999	**0.011**							
Bryozoan 1	>0.999	>0.999	**<0.001**	>0.999						
E modestus	>0.999	>0.999	**0.002**	>0.999	>0.999					
Celleporaria sp 1	>0.999	>0.999	**0.002**	>0.999	>0.999	>0.999				
C foliata	>0.999	>0.999	**<0.001**	>0.999	>0.999	>0.999	>0.999			
C annulata	>0.999	>0.999	**<0.001**	>0.999	>0.999	>0.999	>0.999	>0.999		
B flabellata	>0.999	>0.999	**<0.001**	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	

Table C.16A: Dunn's p values for (Figure 3.21). Recruitment of individual native species and NIS during the 3-month treatments for different seasons Jan-Mar

	W subtorquata	*M membranacea*	*D listerianum*	*C pallasiana*	*C intestinalis*	*B stolonifera*	*B neritina*	*B gracilis*	*B Leachi*	*P stolonifera*	*P taeniatus*	*Obelia sp 1*	*M ficus*
W subtorquata													
M membranacea	>0.999												
D listerianum	>0.999	>0.999											
C pallasiana	>0.999	>0.999	>0.999										
C intestinalis	**0.002**	**0.008**	**0.023**	**0.002**									
B stolonifera	>0.999	>0.999	>0.999	>0.999	**<0.001**								
B neritina	>0.999	>0.999	>0.999	>0.999	**0.001**	>0.999							
B gracilis	>0.999	>0.999	>0.999	>0.999	>0.999	0.338	>0.999						
B Leachi	0.563	>0.999	>0.999	0.444	>0.999	**0.033**	0.146	>0.999					
P stolonifera	>0.999	>0.999	>0.999	>0.999	**0.003**	>0.999	>0.999	>0.999	0.589				
P taeniatus	>0.999	>0.999	>0.999	>0.999	0.110	>0.999	>0.999	>0.999	>0.999	>0.999			
Obelia sp 1	>0.999	>0.999	>0.999	>0.999	**<0.001**	>0.999	>0.999	0.338	**0.033**	>0.999	>0.999		
M ficus	**0.014**	**0.041**	0.113	**0.011**	>0.999	**0.001**	**0.003**	>0.999	>0.999	**0.015**	0.465	**0.001**	
Spirorbid sp 1	>0.999	>0.999	>0.999	>0.999	**<0.001**	>0.999	>0.999	0.338	0.033	>0.999	>0.999	>0.999	**0.001**
Porifera 1	>0.999	>0.999	>0.999	>0.999	**<0.001**	>0.999	>0.999	0.338	0.033	>0.999	>0.999	>0.999	**0.001**
H momus	>0.999	>0.999	>0.999	>0.999	**0.002**	>0.999	>0.999	>0.999	0.522	>0.999	>0.999	>0.999	**0.013**
E modestus	>0.999	>0.999	>0.999	>0.999	**0.002**	>0.999	>0.999	>0.999	0.444	>0.999	>0.999	>0.999	**0.011**
E georgiana	>0.999	>0.999	>0.999	>0.999	**0.001**	>0.999	>0.999	0.957	0.112	>0.999	>0.999	>0.999	**0.002**
Celleporaria sp 1	>0.999	>0.999	>0.999	>0.999	**<0.001**	>0.999	>0.999	0.506	0.053	>0.999	>0.999	>0.999	**0.001**

Table C.16B: Dunn's p values for (Figure 3.21). Recruitment of individual native species and NIS during the 3-month treatments for different seasons Jan-Mar

	Spirorbid sp 1	Porifera 1	H momus	E modestus	E georgiana
Porifera 1	>0.999				
H momus	>0.999	>0.999			
E modestus	>0.999	>0.999	>0.999		
E georgiana	>0.999	>0.999	>0.999	>0.999	
Celleporaria sp 1	>0.999	>0.999	>0.999	>0.999	>0.999

Table C.17: Dunn's p values for (figure 3.21). Recruitment of individual native species and NIS for 3-month treatments for April-June

	W subtorquata	*T crocea*	*T occidentalis*	*M membranacea*	*C intestinalis*	*B gracilis*	*B leachi*	*P taeniatus*	*Obelia sp 1*	*E capillare*
T crocea	>0.999									
T occidentalis	>0.999	>0.999								
M membranacea	>0.999	>0.999	>0.999							
C intestinalis	**<0.001**	**<0.001**	**0.001**	**<0.001**						
B gracilis	**0.004**	**0.002**	**0.003**	**0.003**	>0.999					
B leachi	>0.999	0.561	0.875	0.734	>0.999	>0.999				
P taeniatus	>0.999	>0.999	>0.999	>0.999	**0.040**	0.224	>0.999			
Obelia sp 1	**0.023**	**0.010**	**0.018**	**0.014**	>0.999	>0.999	>0.999	0.784		
E capillare	**0.040**	**0.017**	**0.032**	**0.025**	>0.999	>0.999	>0.999	>0.999	>0.999	

Table C.18: Dunn's p values for (Figure 3.23). Recruitment of sessile and sedentary species for the 6-month settlement treatment for the various species grouping

		Jul-Dec	Oct-Mar	Jan-Jun
All	**Jul-Dec**			
	Oct-Mar	**0.036**		
	Jan-Jun	0.5168	**0.0104**	
	Apr-Sept	**< 0.0001**	**< 0.0001**	**0.0002**
Native	**Jul-Dec**			
	Oct-Mar	**0.0234**		
	Jan-Jun	0.8483	**0.0027**	
	Apr-Sept	**0.0002**	**< 0.0001**	**0.0017**
NIS	**Jul-Dec**			
	Oct-Mar	0.5768		
	Jan-Jun	0.9834	0.3643	
	Apr-Sept	> 0.9999	0.5462	0.9891

Table C.19: Dunn's p values for (Figure 3.24). Recruitment of individual native species and NIS during the 6-month treatments July-December

	W subtorquata	*T occidentalis*	*M membranacea*	*D listerianum*	*C intestinalis*	*B stolonifera*	*B gracilis*	*B leachi*	*P marsupium*	*P taeniatus*	*M ficus*	*Porifera 1*	*Bryozoan 2*	*E capillare*	*E modestus*	*C cervicornis*	*Celleporaria sp*
W subtorquata																	
T occidentalis	>0.999																
M membranacea	>0.999	>0.999															
D listerianum	>0.999	>0.999	>0.999														
C intestinalis	>0.999	>0.999	>0.999	>0.999													
B stolonifera	>0.999	>0.999	>0.999	>0.999	>0.999												
B gracilis	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999											
B leachi	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	0.238										
P marsupium	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	0.423									
P taeniatus	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	0.074	>0.999	0.139								
M ficus	**0.045**	0.539	**0.027**	**0.032**	**0.001**	0.058	**<0.001**	>0.999	**<0.001**	>0.999							
Porifera 1	>0.999	0.859	>0.999	>0.999	>0.999	>0.999	>0.999	0.183	>0.999	0.056	**<0.001**						
Bryozoan 2	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	**0.003**	>0.999					
E capillare	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	0.902	**0.001**	>0.999	>0.999				
E modestus	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	0.807	>0.999	>0.999	>0.999	0.730	0.638	>0.999	>0.999			
C cervicornis	>0.999	0.859	>0.999	>0.999	>0.999	>0.999	>0.999	0.183	>0.999	0.056	**<0.001**	>0.999	>0.999	>0.999	0.638		
Celleporaria sp	>0.999	0.859	>0.999	>0.999	>0.999	>0.999	>0.999	0.183	>0.999	0.056	**<0.001**	>0.999	>0.999	>0.999	0.638	>0.999	
C foliata	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	0.067	>0.999	0.125	>0.999	>0.999	**0.050**	>0.999	0.824	>0.999	**0.050**	**0.050**

Table C.20: Dunn's p values for (Figure 3.24) Recruitment of individual native species and NIS during the 6-month treatments of October-March

	W subtorquata	*T occidentalis*	*C pallasiana*	*C intestinalis*	*B leachi*	*M ficus*	*E modestus*
W subtorquata							
T occidentalis	>0.999						
C pallasiana	>0.999	>0.999					
C intestinalis	0.058	>0.999	**0.023**				
B leachi	>0.999	>0.999	>0.999	>0.999			
M ficus	**<0.001**	**0.002**	**<0.001**	>0.999	**0.004**		
E modestus	>0.999	>0.999	>0.999	**0.023**	>0.999	**<0.001**	

Table C.21: Dunn's p values for (Figure 3.25) Recruitment of individual native species and NIS during the 6-month treatments of Jan-June

	C hemisphaerica	*C intestinalis*	*B gracilis*	*B leachi*	*P taeniatus*	*M ficus*	*E capillare*
C hemisphaerica							
C intestinalis	0.288						
B gracilis	>0.999	**0.002**					
B leachi	>0.999	0.079	>0.999				
P taeniatus	>0.999	**0.034**	>0.999	>0.999			
M ficus	**0.018**	>0.999	**<0.001**	**0.004**	**0.001**		
E capillare	>0.999	0.068	>0.999	>0.999	>0.999	**0.003**	

Table C.22: Dunn's p values for (Figure 3.25) Recruitment of individual native species and NIS, during the 6-month treatments of Apr-Sep

	W subtorquata	*M membranacea*	*D listerianum*	*C hemisphaerica*	*C intestinalis*	*B gracilis*	*B leachi*	*P taeniatus*	*M ficus*	*Porifera 2*	*H momus*	*E capillare*	*E georgiana*
W subtorquata													
M membranacea	>0.999												
D listerianum	>0.999	>0.999											
C hemisphaerica	>0.999	>0.999	>0.999										
C intestinalis	>0.999	>0.999	0.432	>0.999									
B gracilis	>0.999	0.333	**0.008**	0.781	>0.999								
B leachi	>0.999	>0.999	0.646	>0.999	>0.999	>0.999							
P taeniatus	>0.999	>0.999	>0.999	>0.999	>0.999	**0.040**	>0.999						
M ficus	>0.999	>0.999	>0.999	>0.999	>0.999	0.168	>0.999	>0.999					
Porifera 2	>0.999	>0.999	>0.999	>0.999	>0.999	0.066	>0.999	>0.999	>0.999				
H momus	>0.999	>0.999	>0.999	>0.999	0.652	**0.013**	0.958	>0.999	>0.999	>0.999			
E capillare	>0.999	>0.999	>0.999	>0.999	>0.999	0.300	>0.999	>0.999	>0.999	>0.999	>0.999		
E georgiana	>0.999	>0.999	>0.999	>0.999	>0.999	0.191	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	
Celleporaria sp	>0.999	>0.999	>0.999	>0.999	>0.999	**0.030**	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999

Table C.23: Tukey's p values for (Figure 3.?) Percent bare space from three and six month treatments

Treatment	DF	P value
Jul-Sep vs. Oct-Dec	**10**	**p < 0.0001**
Jul-Sept vs. Jan-Mar	**10**	**p < 0.0001**
Jul-Sept vs. Apr-Jun	**10**	p = 0.1463
Oct-Dec vs. Jan-Mar	**10**	p = 0.7521
Oct-Dec vs. Apr-Jun	**10**	**p < 0.0001**
Jan-Mar vs. Apr-Jun	**10**	**p < 0.0001**
Jul-Dec vs. Oct-Mar	**10**	**p = 0.0416**
Jul-Dec vs. Apr-Sep	**10**	p = 0.9657
Jul-Dec vs. Jan-Jun	**10**	p = 0.0554
Oct-Mar vs. Apr-Sep	**10**	**p = 0.0131**
Oct-Mar vs. Jan-Jun	**10**	p = 0.9993
Apr-Sep vs. Jan-Jun	10	p = 0.0580

APPENDIX D

DUNN'S AND TUKEY'S POST HOC TEST VALUES FOR CHAPTER 4

Table D.1: Dunns p values for (Figure 4.3 and 4.4) Settlement frequency of native/NIS epibiotic settlement on native/NIS basibionts across the 3-month treatments, with and without *Molgula ficus* present

		With Molgula				Without Molgula			
		Nat/Nat	**Nat/NIS**	**NIS/NIS**	**NIS/Nat**	**Nat/Nat**	**Nat/NIS**	**NIS/NIS**	**NIS/Nat**
Oct-Dec	**Nat/Nat**								
Oct-Dec	**Nat/NIS**								
Oct-Dec	**NIS/NIS**	0.058				**0.035**			
Oct-Dec	**NIS/Nat**	0.024		**<0.000**		**0.021**		> 0.999	
Jan-March	**Nat/Nat**								
Jan-March	**Nat/NIS**	**0.001**				>0.999			
Jan-March	**NIS/NIS**	**0.026**	>0.999			>0.999	>0.999		
Jan-March	**NIS/Nat**	>0.999	**<0.001**	**0.002**		>0.999	>0.999	>0.999	

Table D.2: Dunns p values for (Figure 4.5 and 4.6) Settlement frequency of native/NIS epibiotic settlement on native/NIS basibionts across the 6-month treatment Oct-Dec with and without *Molgula ficus* present

		With Molgula				Without Molgula			
		Nat/Nat	**Nat/NIS**	**NIS/NIS**	**NIS/Nat**	**Nat/Nat**	**Nat/NIS**	**NIS/NIS**	**NIS/Nat**
Oct-Mar	**Nat/Nat**								
Oct-Mar	**Nat/NIS**								
Oct-Mar	**NIS/NIS**	**0.0202**				**0.0027**			
Oct-Mar	**NIS/Nat**	0.0984		**< 0.0001**		> 0.9999		**0.0011**	
Jan-Jun	**Nat/Nat**								
Jan-Jun	**Nat/NIS**	**0.0077**				> 0.9999			
Jan-Jun	**NIS/NIS**	**0.0072**	> 0.9999			> 0.9999	> 0.9999		
Jan-Jun	**NIS/Nat**	0.7059	**< 0.0001**	**< 0.0001**		0.3902	0.066	0.1938	
Apr-Sep	**Nat/Nat**								
Apr-Sep	**Nat/NIS**	0.1211				0.1211			
Apr-Sep	**NIS/NIS**	> 0.9999	0.1606			> 0.9999	0.1606		
Apr-Sep	**NIS/Nat**	> 0.9999	**0.0051**	> 0.9999		> 0.9999	**0.0051**	> 0.9999	
Jul-Dec	**Nat/Nat**								
Jul-Dec	**Nat/NIS**	**0.0062**							
Jul-Dec	**NIS/NIS**	**0.0198**	> 0.9999						
Jul-Dec	**NIS/Nat**	> 0.9999	**< 0.0001**	**0.0003**					

Table D.3: Dunn's p values for (Figure 4.7) Individual species ratios of settlement for all recorded epibionts recorded from 3-month treatments across all basibionts.

	E georgiana	*E modestus*	*E capillare*	*H momus*	*M ficus*	*Obelia sp 1*	*P irregularis*	*A distains*	*B Leachi*	*B gracilis*	*B flabellata*	*B neritina*	*B stolonifera*	*C intestinalis*	*D listerianum*	*M membranacea*	*O geniculata*	*T occidentalis*
E georgiana																		
E modestus	>0.99																	
E capillare	>0.99	>0.99																
H momus	>0.99	>0.99	**0.021**															
M ficus	>0.99	>0.99	>0.99	>0.99														
Obelia sp 1	>0.99	>0.99	>0.99	**0.035**	>0.99													
P irregularis	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99												
A distains	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99											
B Leachi	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99										
B gracilis	>0.99	>0.99	**0.009**	>0.99	>0.99	**0.014**	>0.99	>0.99	>0.99									
B flabellata	>0.99	>0.99	0.776	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99								
B neritina	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99							
B stolonifera	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99						
C intestinalis	>0.99	>0.99	0.099	>0.99	>0.99	0.159	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99					
D listerianum	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99				
M membranacea	>0.99	>0.99	>0.99	0.340	>0.99	>0.99	>0.99	>0.99	>0.99	0.495	>0.99	>0.99	>0.99	>0.99	>0.99			
O geniculata	>0.99	>0.99	>0.99	0.387	>0.99	>0.99	>0.99	>0.99	>0.99	0.488	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99		
T occidentalis	>0.99	>0.99	0.730	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	
W subtorquata	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99

Table D.4 A: Dunn's p values for (Figure 4.9) Individual species ratios of settlement for all recorded epibionts recorded from 6-month treatments across all basibionts.

	C foliata	*Celleporaria spp*	*C hemisphaerica*	*Darwinella sp*	*E georgiana*	*E modestus*	*E capillare*	*H momus*	*Bryozoa 1*	*M ficus*	*P taeniatus*	*B leachi*	*B gracilis*	*B stolonifera*	*C intestinalis*
C foliata															
Celleporaria spp	>0.99														
C hemisphaerica	>0.99	>0.99													
Darwinella sp	>0.99	>0.99	>0.99												
E georgiana	>0.99	>0.99	>0.99	>0.99											
E modestus	>0.99	>0.99	>0.99	>0.99	>0.99										
E capillare	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99									
H momus	>0.99	>0.99	0.076	>0.99	0.888	>0.99	**0.048**								
Bryozoa 1	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	0.986							
M ficus	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99						
P taeniatus	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99					
B leachi	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99				
B gracilis	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99			
B stolonifera	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99		
C intestinalis	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	
C gigas	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
D listerianum	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
M membranacea	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	**0.050**	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
O geniculata	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
T occidentalis	>0.99	>0.99	0.781	>0.99	>0.99	>0.99	0.647	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99
W subtorquata	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99	>0.99

Table D.4B: Dunn's p values for (Figure 4.9) Individual species ratios of settlement for all recorded epibionts recorded from 6-month treatments across all basibionts.

	C gigas	*D listerianum*	*M membranacea*	*O geniculata*	*T occidentalis*
D listerianum	>0.99				
M membranacea	>0.99	>0.99			
O geniculata	>0.99	>0.99	>0.99		
T occidentalis	>0.99	>0.99	>0.99	>0.99	
W subtorquata	>0.99	>0.99	>0.99	>0.99	>0.99

Table D.5 Tukey's p values for (Figure 4.12). Ratio settlement of native and NIS epibiont on native and NIS basibiont compared to primary bare substrate settlement 3 and 6 month treatments.

		Native/Native	Native/NIS	NIS/Native	NIS/NIS
3-month treatment	**Native/Native**				
3-month treatment	**Native/NIS**	0.9761			
3-month treatment	**NIS/Native**	**0.0024**	0.5435		
3-month treatment	**NIS/NIS**	**0.0034**	0.4418	0.9763	
6-month treatment	**Native/Native**				
6-month treatment	**Native/NIS**	0.8606			
6-month treatment	**NIS/Native**	0.9221	0.9915		
6-month treatment	**NIS/NIS**	0.2181	0.3936	0.9939	

APPENDIX E.

DUNN'S AND TUKEY'S POST HOC TEST VALUES FOR CHAPTER 5

Table E.1: Dunn's p values for (Figure 5.3 and 5.4). Bare space settlement on control versus bare space settlement where basibionts were present of encrusting species

Inoculated species	**Test substrates vs Control**				
	C. bispinata	*C. foliata*	*C. pallasiana*	*S. unicornis*	*W. subtorquata*
C. bispinata	0.0796	0.5737	**0.0339**	**0.0366**	**0.0228**
C. foliata	> 0.9999	0.3499	> 0.9999	> 0.9999	**0.0013**
C. pallasiana	> 0.9999	0.915	0.8532	> 0.9999	**0.0115**
S. unicornis	> 0.9999	> 0.9999	> 0.9999	> 0.9999	> 0.9999
W. subtorquata	> 0.9999	> 0.9999	> 0.9999	0.9781	0.6115
B. dentata	**0.0007**	**0.0011**	**0.0076**	**0.0076**	0.6041
B. neritina	**0.0008**	**0.0031**	0.1665	0.1221	**0.0009**

Table E.2: Dunn's p values for (Figure 5.6). Combined native and NIS ratio settlement on different basibionts

	Celleporaria bispinata	*Celleporaria foliata*	*Cryptosula pallasiana*	*Schizoporella unicornis*
Celleporaria bispinata				
Celleporaria foliata	> 0.9999			
Cryptosula pallasiana	**0.003**	**0.0016**		
Schizoporella unicornis	**0.0002**	**< 0.0001**	> 0.9999	
Watersipora subtorquata	**0.0005**	**0.0002**	> 0.9999	> 0.9999

Table E.3: Dunn's p values for (Figure 5.7) Settlement of bryozoan epibionts on bryozoan basibionts versus control substrate settlement and settlement of bryozoan on space adjacent to basibionts versus control (encrusting species).

		Basibiont ratio				Adjacent ratio			
Inoculant	**Test substrate**	***C bispinata***	***C foliata***	***C pallasiana***	***S unicornis***	***C bispinata***	***C foliata***	***C pallasiana***	***S unicornis***
C bispinata	***C bispinata***								
	C foliata	> 0.9999				> 0.9999			
	C pallasiana	**0.048**	**0.012**			> 0.9999	> 0.9999		
	S unicornis					> 0.9999	> 0.9999	> 0.9999	
	W subtorquata	0.0762	**0.0202**	> 0.9999	> 0.9999	> 0.9999	> 0.9999	> 0.9999	> 0.9999
C foliata	***C bispinata***								
	C foliata	> 0.9999				0.7035			
	C pallasiana	**0.0234**	**0.0005**			> 0.9999	> 0.9999		
	S unicornis	**0.0159**	**0.0003**	> 0.9999		0.2144	> 0.9999	> 0.9999	
	W subtorquata	**0.0199**	**0.0004**	> 0.9999	> 0.9999	> 0.9999	0.4619	> 0.9999	0.1299
C pallasiana	***C bispinata***								
	C foliata	> 0.9999				0.7779			
	C pallasiana	> 0.9999	> 0.9999			0.3843	> 0.9999		
	S unicornis					> 0.9999	0.916	0.4619	
	W subtorquata					**0.0013**	**0.3843**	0.7779	**0.0017**
S unicornis	***C bispinata***								
	C foliata	> 0.9999				> 0.9999			
	C pallasiana	> 0.9999	0.6912			> 0.9999	0.2832		
	S unicornis					> 0.9999	> 0.9999	> 0.9999	
	W subtorquata					> 0.9999	0.1976	> 0.9999	> 0.9999
W subtorquata	***C bispinata***								
	C foliata					> 0.9999			
	C pallasiana	> 0.9999				> 0.9999	> 0.9999		
	S unicornis					0.6135	> 0.9999	> 0.9999	
	W subtorquata	> 0.9999		> 0.9999		0.1191	0.2832	> 0.9999	> 0.9999

Table E.4: Dunn's p values for (Figure 5.8) Settlement of bryozoan epibionts on bryozoan basibionts versus control substrate settlement and settlement of bryozoan on space adjacent to basibionts versus control (arborescent species).

		Basibiont ratio				Adjacent ratio			
Inoculant	Test substrate	***C bispinata***	***C foliata***	***C pallasiana***	***S unicornis***	***C bispinata***	***C foliata***	***C pallasiana***	***S unicornis***
B dentata	***C bispinata***								
	C foliata	> 0.9999				> 0.9999			
	C pallasiana					0.7524	0.9765		
	S unicornis	> 0.9999	> 0.9999			> 0.9999	> 0.9999	> 0.9999	
	W subtorquata	> 0.9999	> 0.9999	> 0.9999		0.2516	0.3432	> 0.9999	> 0.9999
B neritina	***C bispinata***								
	C foliata	> 0.9999				> 0.9999			
	C pallasiana	> 0.9999	> 0.9999			> 0.9999	> 0.9999		
	S unicornis	> 0.9999	> 0.9999	> 0.9999		> 0.9999	> 0.9999	> 0.9999	
	W subtorquata	> 0.9999	> 0.9999	> 0.9999		> 0.9999	> 0.9999	0.5925	0.5146

Table E.5: Dunn's p values for (Figure 5.9) Settlement of individual bryozoan epibionts on bryozoan basibionts versus control substrate settlement and Settlement of bryozoan on space adjacent to basibionts versus control.

		Basibiont ratio						Adjacent ratio					
		C bispinata	*C foliata*	B dentata	B neritina	*C pallasiana*	*S unicornis*	*C bispinata*	*C foliata*	B dentata	B neritina	*C pallasiana*	*S unicornis*
C bispinata	***C bispinata***												
	C foliata	>0.999						>0.999					
	B Dentata	0.441	0.168					**<0.001**	**<0.001**				
	B Neritina	>0.999	0.620	>0.999				**<0.001**	**<0.001**	>0.999			
	C pallasiana	0.332	0.122	>0.999	>0.999			>0.999	>0.999	**0.006**	**0.005**		
	S unicornis	0.057	**0.017**	>0.999	>0.999	>0.999		0.754	>0.999	0.090	0.068	>0.999	
	W subtorquata							0.526	0.957	0.140	0.107	>0.999	>0.999
C foliata	***C bispinata***												
	C foliata	>0.999						>0.999					
	B Dentata	0.085	**<0.001**					**<0.001**	**0.002**				
	B Neritina	0.977	**0.015**	>0.999				**<0.001**	**0.002**	>0.999			
	C pallasiana	0.073	**<0.001**	>0.999	>0.999			0.207	>0.999	0.274	0.301		
	S unicornis	**0.019**	**<0.001**	>0.999	>0.999	>0.999		>0.999	>0.999	**0.006**	**0.007**	>0.999	
	W subtorquata	**0.016**	**<0.001**	>0.999	>0.999	>0.999	>0.999	>0.999	>0.999	**0.018**	**0.020**	>0.999	>0.999
C pallasiana	***C bispinata***												
	C foliata	**<0.001**						>0.999					
	B Dentata	**<0.001**	**<0.001**					**0.001**	**0.003**				
	B Neritina							**0.001**	**0.013**	>0.999			
	C pallasiana	**<0.001**	**<0.001**	**<0.001**				0.066	0.394	>0.999	>0.999		
	S unicornis	0.996	**<0.001**	**<0.001**	0.995			0.220	>0.999	>0.999	>0.999	>0.999	
	W subtorquata	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.995		0.266	>0.999	>0.999	>0.999	>0.999	>0.999
S unicornis	***C bispinata***												
	C foliata							>0.999					
	B Dentata		>0.999					**<0.001**	**0.001**				
	B Neritina		>0.999	>0.999				**<0.001**	**0.005**	>0.999			
	C pallasiana							>0.999	**>0.999**	**0.001**	**0.005**		
	S unicornis							0.360	**>0.999**	**0.041**	**0.150**	>0.999	
	W subtorquata							**0.009**	0.676	>0.999	>0.999	0.658	>0.999

Table E.5: continued

		Basibiont ratio						Adjacent ratio				
		C bispinata	*C foliata*	B Dentata	B Neritina	*C pallasiana*	*S unicornis*	***C bispinata***	***C foliata***	**B Dentata**	**B Neritina**	***C pallasiana***	***S unicornis***
W subtorquata	***C bispinata***												
	C foliata	>0.999						>0.999					
	B Dentata	>0.999	>0.999					**0.007**	**0.007**				
	B Neritina	>0.999	>0.999	>0.999				**<0.001**	**<0.001**	0.714			
	C pallasiana							**0.001**	**0.001**	>0.999	>0.999		
	S unicornis							0.795	0.795	>0.999	**0.006**	0.957	
	W subtorquata	>0.999	>0.999	>0.999	>0.999			0.274	0.274	>0.999	**0.027**	>0.999	>0.999

Table E.6: Dunn's p values for (Figure 5.12) Larval mortality of bryozoan larvae species when inoculated onto a bare control substrate

	C foliata	**C bispinata**	**B dentata**	**B neritina**	**S unicornis**	**C pallasiana**
C foliata						
C bispinata	0.0797					
B dentata	**0.0007**	> 0.9999				
B neritina	> 0.9999	> 0.9999	0.4563			
S unicornis	**< 0.0001**	0.412	> 0.9999	**0.0163**		
C pallasiana	> 0.9999	> 0.9999	0.4697	> 0.9999	**0.0169**	
W subtorquata	**< 0.0001**	**0.026**	> 0.9999	**0.0004**	> 0.9999	**0.0005**

Table E.7: Dunn's p values for (Figure 5.13). Larval mortality (%) of bryozoan species when test substrates are present compared against control substrates

Test larvae	Test basibionts				
	Celleporaria bispinata	**Celleporaria foliata**	**Cryptosula pallasiana**	**Schizoporella unicornis**	**Watersipora subtorquata**
Celleporaria bispinata	0.9901	> 0.9999	**0.0037**	0.979	0.0776
Celleporaria foliata	> 0.9999	0.843	> 0.9999	**0.0395**	> 0.9999
Cryptosula pallasiana	> 0.9999	> 0.9999	0.2321	**0.0072**	**0.0238**
Schizoporella unicornis	> 0.9999	> 0.9999	0.326	> 0.9999	> 0.9999
Watersipora subtorquata	> 0.9999	> 0.9999	0.7362	> 0.9999	> 0.9999
Bugula dentata	0.0846	> 0.9999	0.2392	0.145	0.3751
Bugula neritina	0.2658	0.2056	> 0.9999	0.0594	0.863